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LAJOS BARTUCZ, THE OUTSTANDING PERSONALITY OF HUNGARIAN ANTHROPOLOGY

(Commemoration on the centenary of his birth)

GY. FARKAS

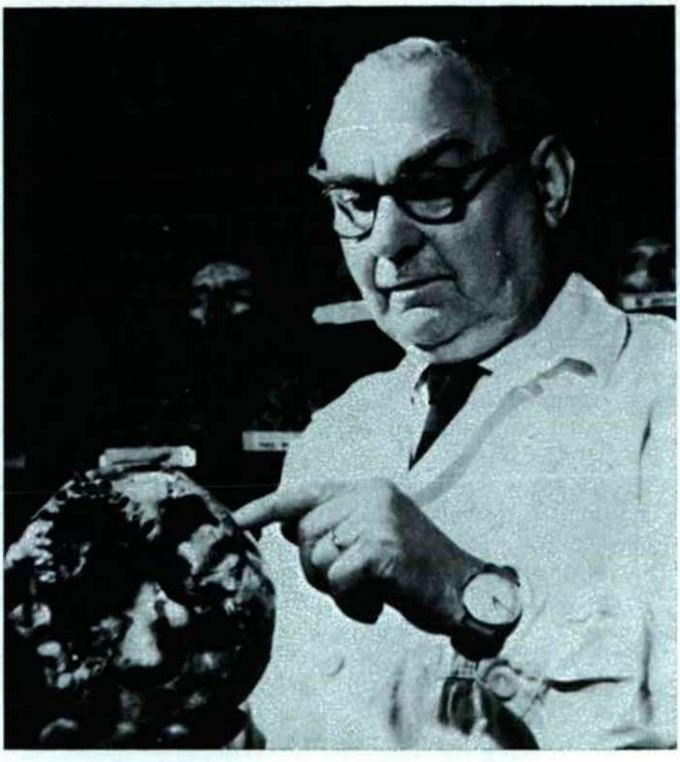
(Received: August 31, 1984)

Abstract

A review is given on the main events in the life of Professor DR. LAJOS BARTUCZ, including his public and scientific activities, the significance of his life-work and its effect on the development of Hungarian anthropology. The relevant bibliography related to LAJOS BARTUCZ and his scientific activities are also presented.

All this is in connection with the fact that the centenary of the birth of Professor BARTUCZ will be on April 1, 1985.

Keywords: LAJOS BARTUCZ, Hungarian anthropology, commemoration.



LAJOS BARTUCZ was born on April 1, 1885 in the village Szegvár located in Southern Hungary. He wrote in one of his biographies: "My father was a manorial servant at Mágocs, my mother was a peasant girl. With his ability and unwearied industry, my father attained becoming a fire-tender at the manorial heater and later he became a machinist. My mother inherited two acres of land so they became small land-owners at Szegvár".

He finished his primary school with excellent result at Szegvár. Then he was enrolled to the Piarist gymnasium in Kecskemét. During the Summer holiday he stoked the threshing-machine and took part in all kinds of agricultural work with his brother, who was a locksmith and machinist.

Since his father was unable to send him to school due to aridity lasting for several years, after finishing the VI. form at gymnasium he was put to the Piarists as a student. This is how he arrived at Vác and then in Budapest for finishing the VII.—VIII. forms of the gymnasium. In 1904 he passed his exams with very good results after which he matriculated at the PETER PÁZMÁNY University of Sciences in Budapest to the faculty of natural sciences and geography. He finished his studies there as a student between the years 1904 and 1908. He already dealt with anthropology as a first-year university student and since he did not want to become a monk, AURÉL TÖRÖK — head of the Institute of Anthropology in Budapest at that time — who saw his interest towards anthropology, appointed him to the university as an assistant, thus he left the Piarists.

Between 1905 and 1909 he worked at the Budapest University of Sciences as an assistant and in the first term of the 1908/1909 session while AURÉL TÖRÖK was ill — he held lectures for the students. His first scientific paper appeared in 1905.

In 1908 he passed his examination for doctorate in philosophy with "summa cum laude" on the subjects of anthropology, zoology and geology.

In June, 1909 he became a research student, then assistent from October 1, in the same year and assistent lecturer from June 16, 1914. He was qualified as lecturer and became the private-docent of anthropometry on August 4, 1914.

In 1919 he taught anthropology, social anthropology and origin of mankind at the MARX—ENGELS Workers' University. In June of the same year the People's Committee of Public Education of the Hungarian—Soviet Republic entrusted him with organizing a Department of Anthropology within the frame of the Museum of Natural Sciences. This brilliant plan, however, could not be realized during the short period of the Soviet regime. In the September of 1920, he was removed from his post as university assistant lecturer and he wasn't even allowed to enter the Institute to work.

From 1920 to 1926 were difficult years for LAJOS BARTUCZ. For several years he vegetated on manufacturing shoe-polish, floor-polish, dye for clothes and other housewares. During this period, however, he often went to the Museum of Ethnography where he was entrusted with arranging the anthropological collection and later with the organization of the Department of Anthropology. He was charged with the commission as professional clerk here on February 16, 1924, and became guard at the Museum from June, 1926. Later, in July, 1935 he became first-class guard, then acting director from February, 1936 and director of the Museum from June, 1938.

At the Museum of Ethnography he organized an anthropological collection

which by virtue of his methodologically collected findings, became famous throughout Europe.

During the years spent at the Museum of Ethnography he held a limited number lectures at the University as honorary lecturer and in 1933 — after the retirement of LAJOS MÉHELY — he was entrusted with holding lectures on anthropology as well as with the scientific leadership of the Institute at the University of Sciences in Budapest.

In 1936 he organized a Hungarian anthropological exhibition in Vienna, where he displayed the history of Hungarian anthropological researches, the composition according to race of the Hungarians and the people living earlier in the Carpathian-basin, and the significance of these researches from the point of view of the ethnogenesis of Eurasia. Although the foreign daily papers and scientific societies spoke highly of this exhibition, LAJOS MÉHELY — who was the chairman of the political screening committee in 1920 when LAJOS BARTUCZ was removed from his post — denounced him and balked his appointment to professorship, despite the fact that he was proposed for this post by the Budapest University of Sciences in 1939.

It meant a significant turn in the life of LAJOS BARTUCZ that on October 19, 1940, he was appointed to university professor and director of the Institute of Anthropology established at that time at the University of Sciences in Szeged. He founded the scientific institute at the Great Hungarian Plain in 1940, the objective of which was the scientific processing of the natural and ethnographic sources of the Southern Lowlands.

Following his appointment he received several assignments at the University. Thus he was the Dean of the Faculty of Natural Sciences in the 1943/1944, 1944/1945 and 1945/1946 sessions, member of the National Board of University Education between 1943 and 1949, president of the State Board of Examiners for Candidates to Secondary-Schoolmastership in Szeged from the 1945/1946 to the 1947/1948 school years, president of the University Screening Committee of the Trade Union in 1945/1946, and vice-president of the University Economic Commitee between 1944 and November, 1946.

When due to the events of the war of 1944 the majority of the university teaching staff left for Budapest, he stayed in Szeged even in the most difficult periods, intensively taking part in the salvage of the University's properties and in the earliest possible recommencement of the lectures. The lines cited from the letter of LÁSZLÓ TÓTH, Rector of that time, written to LAJOS BARTUCZ on November 22, 1946 cast light on his activities: "On the occasion of the III. ordinary assembly held on November 19, 1946, the Council of our University was pleased to be informed from the official communication of the University's Economic Committee that during the Autumn of 1944, when the University was in critical situation due to events of the war, the Economic Committee constituted from the director of the Economic Office and the professors staying in Szeged did its best to ensure the life of the University even amidst the severe and many times insurmountable difficulties. It is particularly owing to the Professor, the vice-president of the Committee, that by his generous work, unsparing in efforts, the Committee was able to do this difficult work with excellent results and was capable of promoting the development of the University from its past futureless, often hopeless, situation".

Professor BARTUCZ was the leader of the Institute of Anthropology at the Szeged University till February 2, 1959, following this he was appointed to be the director of the Institute of Anthropology of the LÓRÁND EÖTVÖS University of Sciences in

Budapest. With this appointment he filled the leading post which was vacant since 1913. He worked here till his retirement on February 28, 1965.

He died in Budapest on June 4, 1966 at the age of 81.

LAJOS BARTUCZ did not belong to the "travelling scientists", nevertheless — especially in his younger years — he took part in foreign congresses despite his difficult financial conditions.

In 1915 he worked for three months with Professor PÖCH in Vienna, but he also went on study-tours in Munich at RANKE and in Zurich at SCHLAGINHAUFEN.

He held lectures at the Anthropological Congresses in Vienna (1927), Salzburg (1927), Paris (1931), Helsinki (1932), London (1934), Bucarest (1937) and Coppenhagen (1938). In Prague, 1962, he participated in the Conference of the Preliminary Committee of the International Anthropological and Ethnological Congress held in Moscow (1962). He was asked by the Slovakian Academy of Sciences to deliver lecture in Bratislava on the life and activities of AURÉL TÖRÖK.

He was a member and functionary in several Hungarian societies; scientific secretary-general and managing chairman of the Hungarian Society of Ethnography, co-chairman and later honorary member of the Hungarian Society of Biology, vice-president of the General Committee of Anthropology of the Biological Section of the Hungarian Academy of Sciences, president of the Anthropological Section of the Hungarian Society of Biology.

Among the foreign societies, his honorary membership in the permanent committee of the International Anthropological and Ethnological Congress should be mentioned (1962).

According to LAJOS BARTUCZ three conditions are necessitated for having a science revive in a country: a university platform where the subject is taught, a scientific society where the results are discussed, and a scientific periodical where these are published. LAJOS BARTUCZ did his best in the interest of having all three conditions realized in Hungarian anthropology. He started editing the periodical called Anthropological Periodicals (Anthropologia Hungarica) in 1923, and althrough not many volumes were published during its existence till 1939, several articles were published in them. Between 1940 and 1949 he was the editor of the Yearbook of the Scientific Institute of the Great Hungarian Plain and he was also a member of the editorial Board of Acta Biologica Universitatis Szegediensis and Anthropological Communications, in which many of his anthropological studies appeared.

His field of research was rather wide. Nevertheless, it could be said that he was firstly interested in historical anthropology, ethnical anthropology (the anthropology of the Hungarians), the growth and development of children and the origin of man. His educational activities were also outstanding. The intensity of his work is shown by 12 larger publications (university lecture notes, monographs, special anthropological books) and over 230 essays which refers to the fact that he published the results of his research with pleasure. When mentioning his name we cannot leap over such unique research as the exhumation of the bones MIHÁLY APAFI, the martyrs of Arad, IGNÁC MARTINOVICS and his companions, GÜL BABA, JÓZSEF KATONA and his family, IGNÁC SEMMELWEIS, TIVADAR KOSZKA CSONTVÁRI, SÁNDOR LŐWI martyr.

His activity was acknowledged by foreign as well as Hungarian orders. In 1931 he was awarded the BAUMGARTEN prize for the impartial representation of scientific justice and for the cultivation of popular science on literary level. In 1952 he obtained the degree of Doctor of Biological Sciences from the Hungarian Academy of Sciences

as the acknowledgement of his activities. In 1960 he became Doctor of 50 years' standing and in 1965 — at the time of his retirement — he was awarded the Golden Degree of the Order of Labour by the Hungarian Government.

LAJOS BARTUCZ did not create a scientific school in the strict sense of the word, but his lectures held in captivating style and his lessons imbued with personal experience apprehended many students. It is not accidental that many regard him as their master from the outstanding representatives of Hungarian anthropology who have deceased since then (MIHÁLY MALÁN, MIKLÓS FEHÁR), or have retired (JÁNOS NEMESKÉRI, PÁL LIPTÁK), as well as from the present active representatives (GYULA DEZSŐ, the author of these paper); but he also had many followers indirectly. Beyond his lectures his extremely enjoyable style and his publications on a rather wide variety of topics captivated his listeners and so it could be said that the succeeding generations can respect him as one of the founders of today's Hungarian anthropology. The establishment of two collections is also linked to his name (one at the Anthropological Cabinet of the present-day Museum of Natural Sciences, the other at the Department of Anthropology of the ATTILA JÓZSEF University in Szeged which are also significant in Europa). FERENC MÓRA was of great help to him in this, who by handing over his collection of firstly prehistoric findings, established the today's collection at Szeged.

His disciples were fond of and respected him, they presented him with a memorial-plaque on the 80th anniversary of his birthday.

With this commemoration we wish to pay our respects to the memory of the great scientist of the Hungarians, the outstanding representative of Hungarian anthropology, on the occasion of the centenary of his birth.

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ACETYLCHOLINESTERASE ACTIVITY MEASUREMENTS AS A TOOL FOR DEMONSTRATING THE POSSIBLE CAUSE OF FISH DECAY

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(Received: June 30, 1984)

Abstract

Mass decay occurred in November 1982 in the fish ponds of the 'Eastern Light' Agricultural Co-operative at Pálmonostora, located in the area of the Water Conservancy Directorate of the Lower Tisza Region (Southern Hungary). The temperature of the water was 8 °C, the solved 0_2 content was 4.2 mg/l. Biochemical studies on the organs of 6—700 g carps (*Cyprinus carpio* L.) brought in from the scene of the occurrence demonstrated that one of the possible causes of the mass fish decay might be due to the inhibition of acetylcholinesterase (AChE, EC 3.1.1.7.) by some kind of water pollution. The degree of inhibition in the heart and muscle was 50—60% and 80—90% in the brain and heart respectively.

Key words: fish, acetylcholinesterase, water pollution.

Introduction

Measurements on the changes in enzyme activity of acetylcholinesterase (AChE, EC 3.1.1.7.) have been used for a long time determining the characteristic toxic effect of insecticides containing organic phosphate and of carbamate type (GAGE, 1955; O'BRIEN, 1960; HEAT, 1961; GAGE, 1967). It has also been demonstrated in the case of fish that water contamination may also cause damage in the nervous system through the inhibition of acetylcholinesterase (HOLLAND et al., 1967; COPPAGE et al., 1975; COPPAGE and BRAIDECH, 1976; KLAVERKAMP et al., 1977; KLAVERKAMP and HOBDEN, 1980; HANKE et al., 1983; NEMCSÓK et al., 1984).

Taking the above into cinsideration studies were carried out on still living fish collected from the site of mass fish decay occurring in November, 1982. The purpose of the studies was to determine possible tissue damage, and injury of the nervous system, respectively, in the fish regarding the changes in the enzyme activity of aminotransferase (glutamic acid-oxalacetic acid-transaminase, GOT: EC 2.6.1.1.; glutamic acid-pyruvic acid-transaminase, GPT: EC 2.6.1.2.) in the serum as well as of acetylcholinesterase in the various organs.

Materials and Methods

1. THE SPOT AND CONDITIONS OF THE FISH DECAY

The fish decay was observed on November 4, 1982 in the fish ponds of the 'Eastern Light' Agricultural Co-operative at Pálmonostora. Arriving on the spot, the specialist of the Water Conservancy Directorate of the Lower Tisza Region found a large number of perished, just living fish

in the so-called „winter fish ponds". The temperature of the water was 8 °C, the solved O_2 content was 4.2 mg/l at dawn. Three 6—700 g carps from the still living individuals were taken to the Department of Biochemistry Attila József University for studies. Blood was taken from the tail vessels of the fish, centrifuged and the activity of the GOT and GPT enzymes as well as of the AChE enzyme was measured from the blood plasma. The adequate data of healthy carps kept at identical water temperature and of the same weights were used as controls.

2. Measurements applied for the biochemical studies

2.1. *Determination of the GOT and GPT activities*

One part of the oxalacetic acid formed during the course of the catalysed reaction by these transaminases spontaneously transformed into pyruvic acid, which latter formed coloured complex with 2.4-dinitrophenyl-hydrasine in alkalinic medium, the light-absorption of which was measured.

a) *Reaction mixture used for determining GOT*

0.25 ml 0.1 M phosphate buffer (pH=7.4) containing 0.1 M L-asparagine acid and 2 mM alpha-ketoglutaric acid +0.05 ml blood serum. (The blank sample contained the same amount of destilled water).

b) *Reaction mixture used for determining GPT*

0.25 ml 0.1 M phosphate buffer (pH=7.4) containing 0.2 M DL-alanine and 2 mM alpha-ketoglutaric acid +0.05 ml blood serum. (The blank sample contained 0.05 ml destilled water After incubation at 37° C for 60 min/for 30 min. in the case of GPT) 0.25 ml 1 mM 2.4-dinitrophenyl-hydrasine was added to each sample and the reaction mixture was left for 20° C, then after adding 2.5 ml 0.4 M NaOH the extinction was measured at 540 nm. The activity was expressed in U/1 used and accepted in toxicology (1 U = µmol decomposed substrate) (1 min at 25° C).

2.2. *Determination of acetylcholinesterase with the method of Ellman et al. (1961)*

The acetylcholinesterase enzyme hydrolized the acetylcholine-iodide to thiocholine and acetic acid. The —SH group of thiocholine gave colour reaction with dithio-bis-nitro-benzoic acid (DTNB). The reaction mixture was: 2 ml 52 mM phosphate buffer (pH=7.2) containing 0.26 mM DTNB). 0.05 ml acetylthiocholine-iodide of 82.4 mM+0.01 ml blood serum. Reaction was started by adding blood serum which was registrated for 3 min at 412 nm by light absorption. (The change was linear within this time). Activity was expressed in U/1.

Results and Discussion

In the collected carps the blood vessels were well observable at the lower part of the abdomen, the movement of their opercule was irregular, their posture was numb, jerky. The aminotransferase enzyme activities measured from the blood plasma were of similar values as the control, however, the AChE activities of the blood plasma showed considerable decrease compared to the values of the control individuals (Table 1). The AChE activity also significantly decreased in the organs of the fish

Table 1. Values of serum transaminase activity in control carps and carps originating from polluted water at the time of the fish decay observed in Csongrád county.

Sample	GOT (U/1)	GPT (U/1)
Still living carps collected from the area of the fish decay (3 individuals)	28.3±3.5	1.27±0.31
Control carps (10 individuals)	32.4±18.8	1.38±0.63

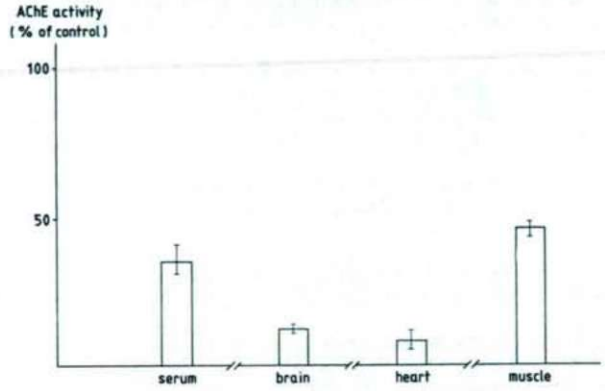

Fig. 1. The acetylcholinesterase activity in different organs of carp. Fish were collected from pesticide polluted water. Values are expressed in the percentage of „healthy" fishes, collected from non polluted water.

(Fig. 1.). The inhibition of acetylcholinesterase in the various organs of fish is harmful from several points of view.

1. It inhibits the normal nerve function and the various vital behaviour functions which are essential in obtaining food as well as in the defensive, escaping reactions (ABOU—DONIA and MENZEL, 1967; BASLOW and NIGRELLI, 1961; COPPAGE, 1971).

2. The inhibition of acetylcholinesterase is especially dangerous in the heart, since the cholinergic system has decisive role in the innervation of the hearts in fish (PENNEC and LA BRAS, 1984): inhibition of acetylcholinesterase may lead to the increase of vagus effect, which may cause severe disturbances in the metabolism-process related to the circulation. This is so, since the inhibition of the heart function has harmful effect on the O_2 uptake and CO_2 release, thus it may cause anoxia at the tissue level. On the basis of our results, the acetylcholinesterase inhibition might also have played role in the fish decay. The cause of this was presumably the insecticide or other type of chemicals used in the environment of the fish ponds which may cause acetylcholinesterase inhibition of significant degree even at rather low concentrations (COPPAGE, 1971, 1972; COPPAGE and MATTHEWS, 1975; COPPAGE et al., 1975; COPPAGE and BRAIDECH, 1976; KLAVERKAMP et al., 1977; DUANGSAWASDI and KLAVERKAMP, 1979; KLAVERKAMP and HOBDEN, 1980; NEMCSÓK et al., 1984).

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BIOCHEMICAL, FLUORESCENCE MICROSCOPIC AND ULTRASTRUCTURAL STUDIES ON BIOGENIC MONOAMINES IN THE GUT OF HELIX POMATIA

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Abstract

Authors studied the innervation of the gut in *Helix pomatia* with simultaneous chemical, fluorescence microscopic and electron microscopic methods. On the basis of the chemical measurements it was determined that adrenaline, noradrenaline, dopamine and serotonin are all present in the snail gut in a significant amount. Serotonin was demonstrable in the largest amount (1.26 µg/g wet weight), at the same time, the amount of noradrenaline was lower by two orders (0.05 µg/g wet weight). The fluorescence microscopic studies confirmed the results of the chemical determination and demonstrated a large amount of fluorescent fibres, fibre bundles and neurons in the complete intestinal tract. Electron microscopically neurons, synaptic neuropil and terminal nerve fibres were found in the snail gut muscle. Dense-core vesicles with diameters of 100 nm were observed both in the nerve cell bodies and the axon terminals directly neighbouring the muscle fibres.

The observations obtained by the above complex methods serve unambiguous evidence for the aminergic innervation of the snail gut.

Key words: Helix pomatia, gut, biogenic monoamine, fluorescence studies, ultrastructure.

Introduction

The scientific interest towards molluscs, and within this snails has been increased significantly in last few decades. Besides scientific viewpoints, there are also economical causes of this interest: snails are valuable export goods and they are also animals causing damage in agriculture and so they, cannot be underestimated. From scientific point of view snails have particularly proved to be good test objects for neurobiological researches, as large, well accessible neurons have been found in the central nervous system, which have been used for complex neurophysiological and neuromorphological studies. The majority of the neurobiological studies have been done on the central nervous system (ELEKES, 1983; KISS et al., 1977; OSBORNE et al., 1982; S-RÓZSA et al., 1974), but studies have also been continued on the peripheral nerve areas (BENEDECZKY, 1977; ERDÉLYI et al., 1972; HERNÁDI et al., 1983; KISS et al., 1982; S-RÓZSA et al., 1964).

ÁBRAHÁM (1940) had turned his attention to the rich innervation of the snail gut quite a long time ago. Despite this, the first ultrastructural studies (ÁBRAHÁM, 1983; HALASY et al., 1983; TÁNCZOS et al., 1979) had only commenced with great delay, but supported well the early light microscopic observations. During the course of electronmicroscopic studies nerve cell bodies and large amounts of nerve terminals were found between the muscle fibres. On the basis of the ultrastructural characteristics HALASY et al. (1983) separated 3 types of nerve terminals. The majority of the

terminals contained neurosecretory granules therefore it was assumed that these correspond to peptidergic terminals. Nerve terminals containing dense-core vesicles were also detected, which were thought to originate from aminergic neurons. All these facts rendered the occurrence of aminergic innervation in the snail gut probable, thus the present study carried out by biochemical measurements and fluorescence microscopic studies simultaneously, aimed to verify the presence of aminergic innervation and concluding from this we wish to discuss its possible role in the regulation of the intestinal activity.

Materials and Methods

I. Electronmicroscopy

Our studies were carried out on mature *Helix pomatia* L. *(Mollusca: Gastropoda)* individuals collected from humid meadows at the environs of Szeged in Summer, 1983. The animals were dissected and the 1 mm^3 sized pieces cut from the various sections of the intestinal tract were fixed in cold state in 2.5% glutaraldehyde diluted with phosphate buffer, resp. Karnovsky-fixative, for 2 hours besides 7.3 pH. Then the tissue blocks were washed in phosphate buffer containing 7.5% saccharose, then postfixed in 2% osmium tetroxide set to 7.5 pH with phosphate buffer for 2 hours at 4 °C. Then the material was dehydrated in ascending alcohol series. The tissue blocks were contrasted with saturated uranyl acetate in 75% ethanol in dark for 1 hour. The blocks were embedded in Spurr-embedding material and then sections prepared, recontrasted with lead citrate and then studied under TESLA BS 500 electronmicroscope.

II. Fluorescence microscopic studies

The saccharose-phosphate-glyoxylic acid (SPG) method (de la Torre et al., 1976) was used for the histochemical demonstration of the monoamines. The alimentary tract was dissected in whole length or in small pieces, then incubated in the reaction mixture containing 6.8 gr saccharose, 3.2 g KH_2PO_4 and 1 g glyoxylic acid at 4 °C for 15 min. At the end of the incubation period the submucous layer was stripped off, the muscle layer was stretched out on slides, the moisture removed by blotting paper and the specimens dried by cold air for about 1/2 hour. The completely dry samples were treated with heat for 4 min. at 95 °C. The preparations were covered with paraffin oil and studied with Leitz Orthoplan microscope equipped with indirect illumination and HBO 50 high-pressure mercury-vapour lamp. Green fluorescence characteristic of catecholamines was detected by applying E-3 filter-block. Pictures were prepared on FORTE-PAN 400 ASA black and white film. The control preparations were treated as described previously, but glyoxylic acid was left out of the reaction mixture.

III. Chemical Studies

Adrenaline and noradrenaline were determined according to the fluorimetric method of Anton and Sayre (1962), the dopamine measured according to Schellenberger and Gordon (1971) and serotonin demonstrated according to Snyder et al. (1965). Perkin—Elmer HPF-44B type fluorescence spectrophotometer was used for the measurements.

Results

I. Electronmicroscopy

One of the types of the nerve fibres occurring in the smooth muscle layer of *Helix pomatia* gut contains so-called large dense-core vesicles, the average diameters of which were 100 nm. During the course of the present study attention was paid to these nerve fibres and terminals, thought to be aminergic on the basis of the literary data (Gabella, 1979; Mercer et al., 1981). Such nerves could frequently be observed

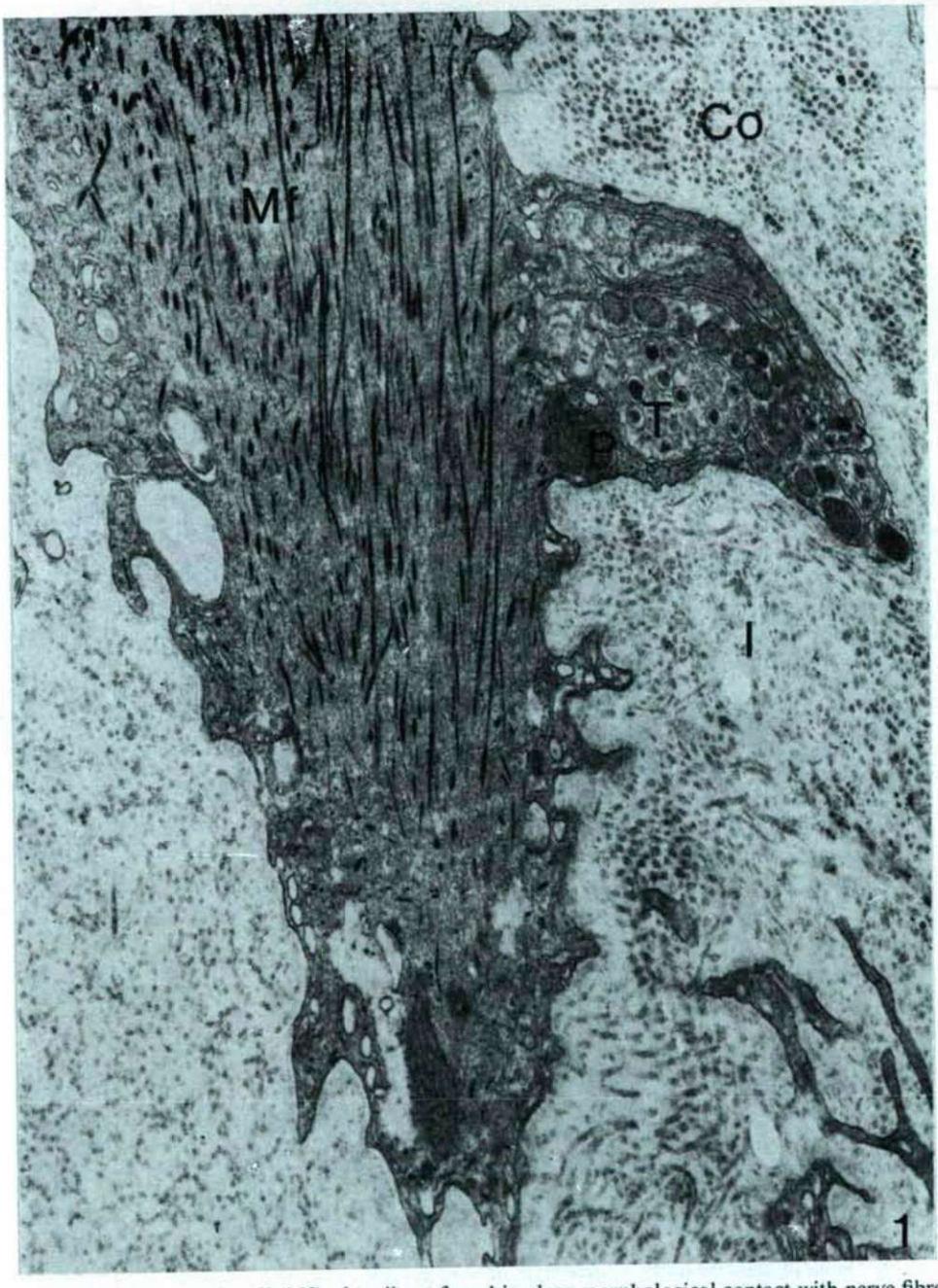


Fig. 1. Smooth muscle cell (Mf) of snail gut found in close morphological contact with nerve fibre (T) containing dense-core vesicles. The muscle fibre admits a mitochondrium-containing process (P) towards the terminal. I = interstitium, Co = collagen fibre ×20 000

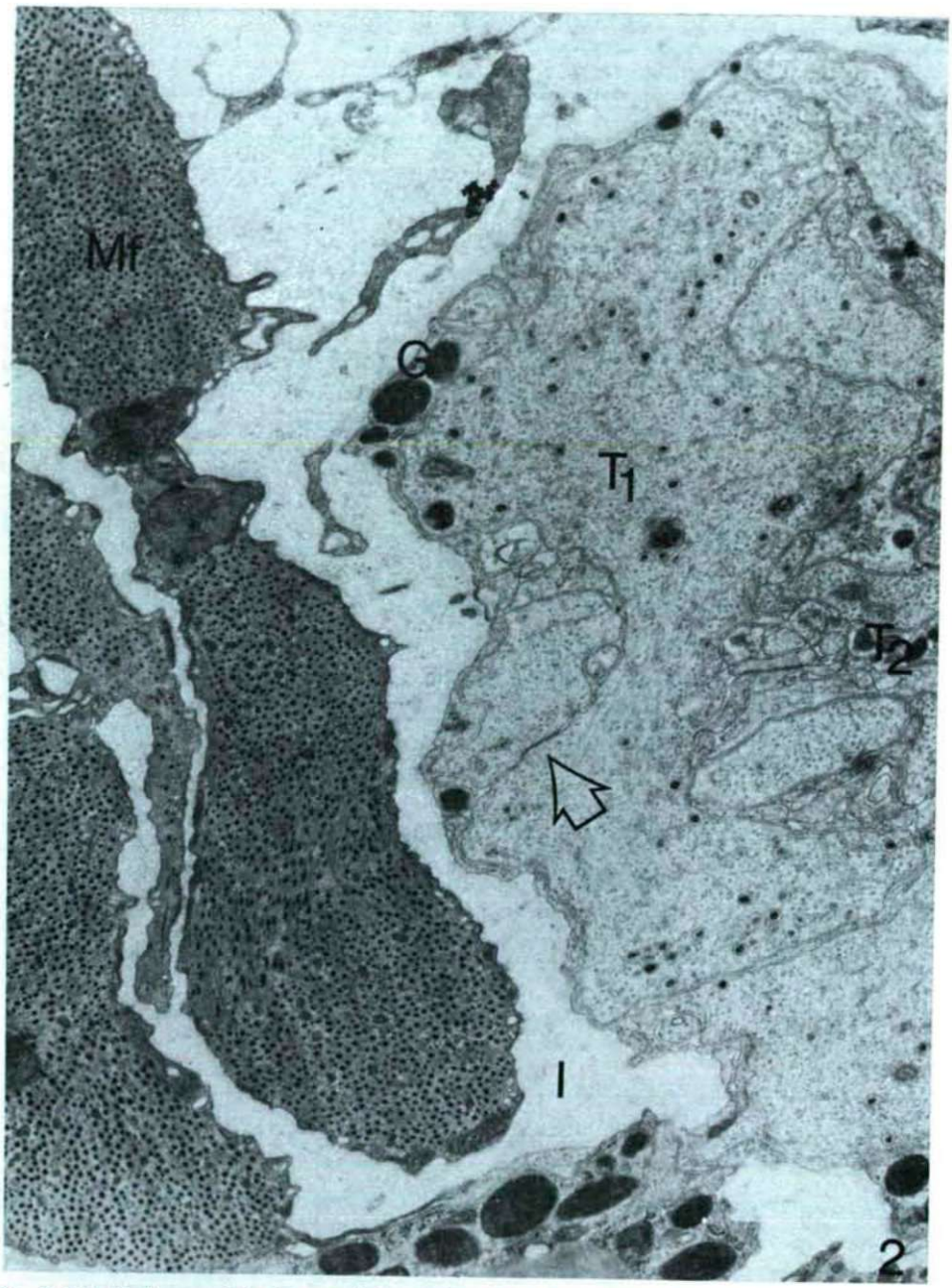


Fig. 2. Detail of neuropil in the muscle layer of snail gut. Mf = smooth muscle cell, T_1 = dense-core vesicle-containing nerve fibre, T_2 = nerve fibre containing neurosecretory granules, I = interstitium, G = glial process with glial granules. The arrow points to a close junction between two nerve fibres. ×15 000

in the direct neighbourhood of the smooth muscle fibres (Fig. 1), as well as in the neuropil (Fig. 2). The terminals — which lost their glial covering and the number of dense-core vesicles increased in them — were usually in tight morphological contact with the processes of smooth muscle cells, which also contained mitochondria (Fig. 1). The sarcolemma and the terminal membrane attached on large surfaces, but neither of them showed synaptic membrane specialization.

The nerve fibres of similar type found in the neuropil (Fig. 2) contain dense-core vesicles in relatively lower amount than in the terminals, however, a significant amount of microtubuli and neurofilaments can be found in them. The surface of the nerves facing to the interstitium was covered by glial processes. Up to now, synaptic connections could not be observed among the nerves situated within the neuropil.

In the interstitium between the muscle fibres neurons were also found, the perikaryon of which also contained large amounts of dense-core vesicles (Fig. 3). On the basis of the vesicle-type similarity, the above-mentioned nerves could be regarded as the processes of these neurons. The most characteristic organelles of the cells were the rough surfaced endoplasmic reticulum as well as the Golgi-apparatus, in the cisternae of which material of similar density to the contents of the dense-core vesicles could be observed, especially at higher magnification (Fig. 3. insert). It was also characteristic to these cells that mitochondria were present in large amounts. Quite frequently other types of fibres, containing neurosecretory granules could be observed close to the soma (Fig. 3. arrow).

II. Fluorescence microscopic studies

The histofluorescence characteristic to monoamines only appeared in the samples treated with glyoxylic acid. This means that the observed fluorescence really originated from the monoamines present in the tissues. Regarding the fluorescence intensity and the distribution of the fluorescent nerve elements three main segments were found in the snail gut.

In the foregut an extremely rich network of the green fluorescent nerve elements was observed (Fig. 4). The fluorescence was rather intensive and well localized. One part of the fluorescent fibres had independent course in the form of thin varicose fibres (Fig. 4. arrow), while at other places the fibres were arranged in thick bundles (Fig. 4., 5. arrow heads). Nerve cell bodies of various sizes and shapes were observed in close connection to the nerve bundles (Fig. 4., 5. filled arrows). At some places single, strongly fluorescent cells were also seen with no visible connection to nerve fibres. These were uniform in size, but varied in shape (Fig. 6., 7a, b). In most of the cells the fluorescence intensity was the same on the whole cell surface (Fig. 6., 7a), while in a few cases the fluorescence was not observed above the nucleus (Fig. 7b). The fluorescence intensity of the nerve fibres running in the stomach was lower than in the foregut, and formed a loose network (Fig. 9). Around the fibres a large number of relatively small cells were observed in which the fluorescence was limited to the cytoplasm (Fig. 9a). These cells were very uniform regarding both size and shape, all of them appeared to be unipolar. Most of the hindgut fibres were thin and varicose (Fig. 8). The fluorescence of the fibres were localized, but the intensity was lower than that of experienced in the foregut. Fluorescent cell bodies were only rarely observed in this part of the gut.

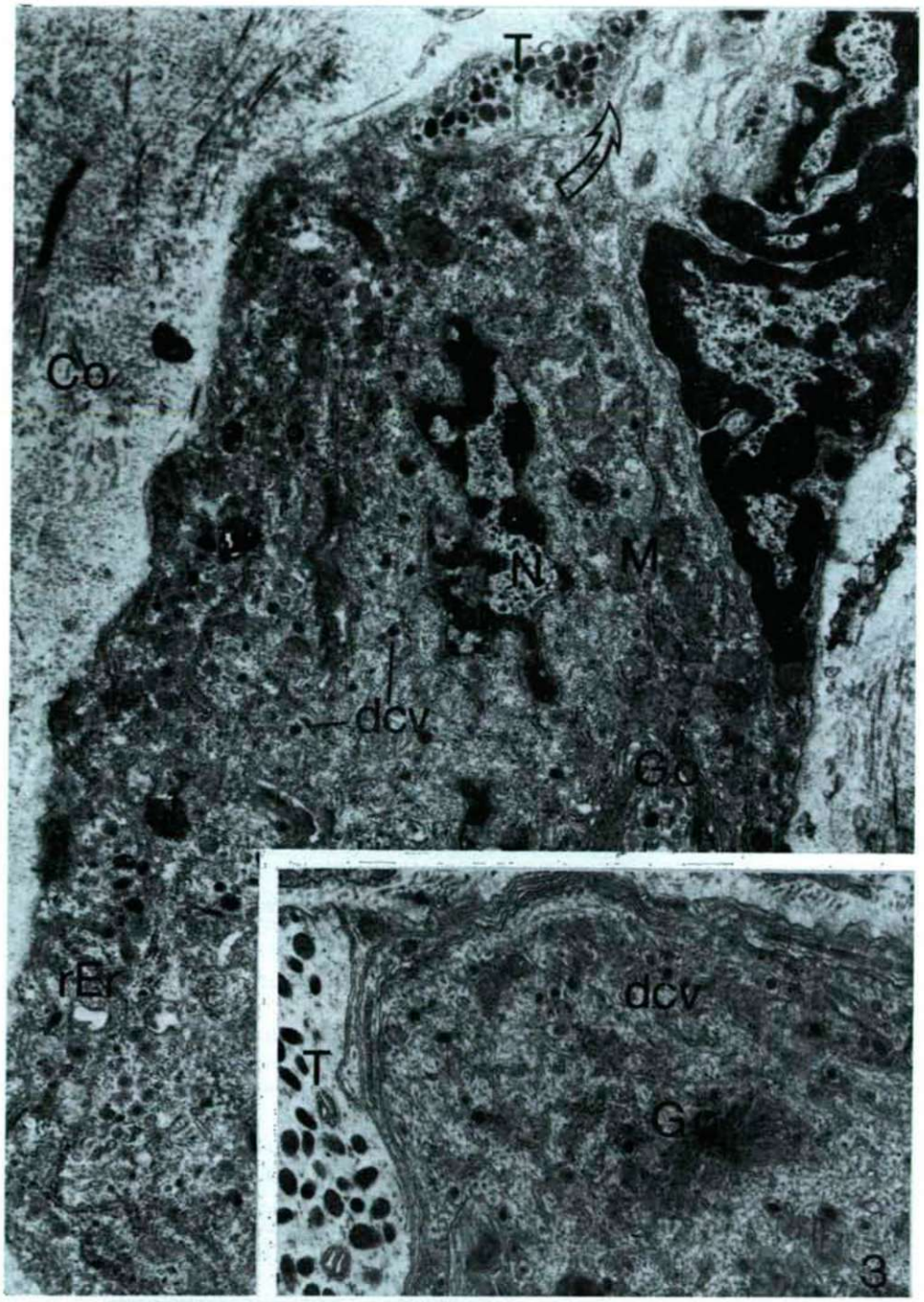
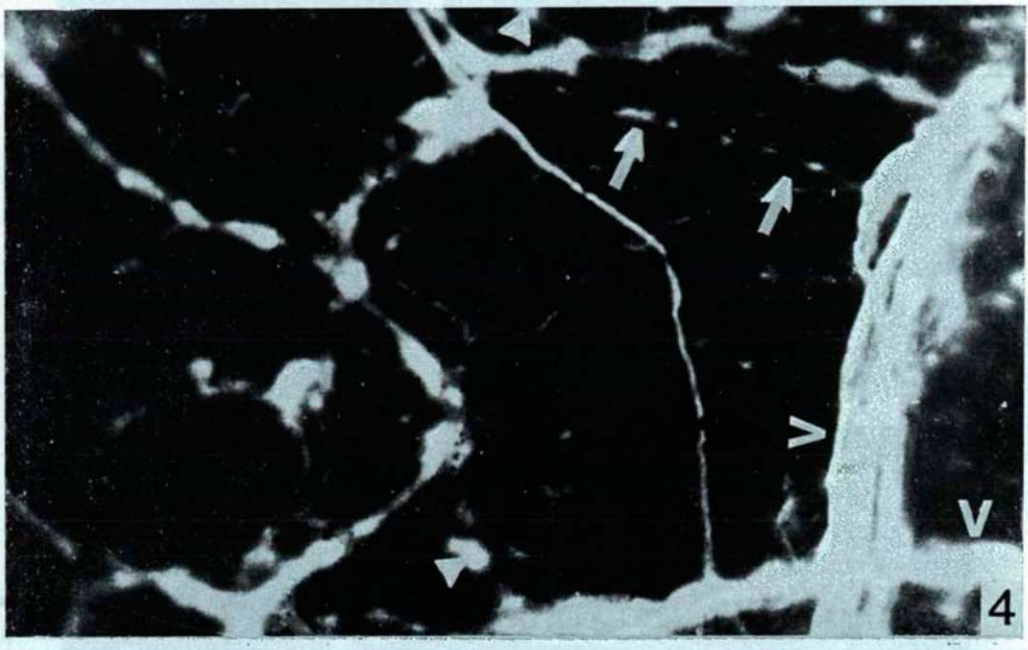


Fig. 3. Intramural neuron from the gut muscle of snail. Dense-core vesicles can be seen in the perikaryon (dcv). N=nucleus, rEr=rough surfaced endoplasmatic reticulum, Go=Golgi-apparatus, M=mitochondrium. The arrow indicates the close junction between the neuron and a nerve fibre (T) containing neurosecretory granules. Co=collagen fibres ×15 000
Insert: Magnified detail of a similar neuron with dense-core vesicles (dcv) and well developed Golgi-apparatus (Go). A nerve fibre (T) of the neurosecretory type is observable besides the cell. ×30 000



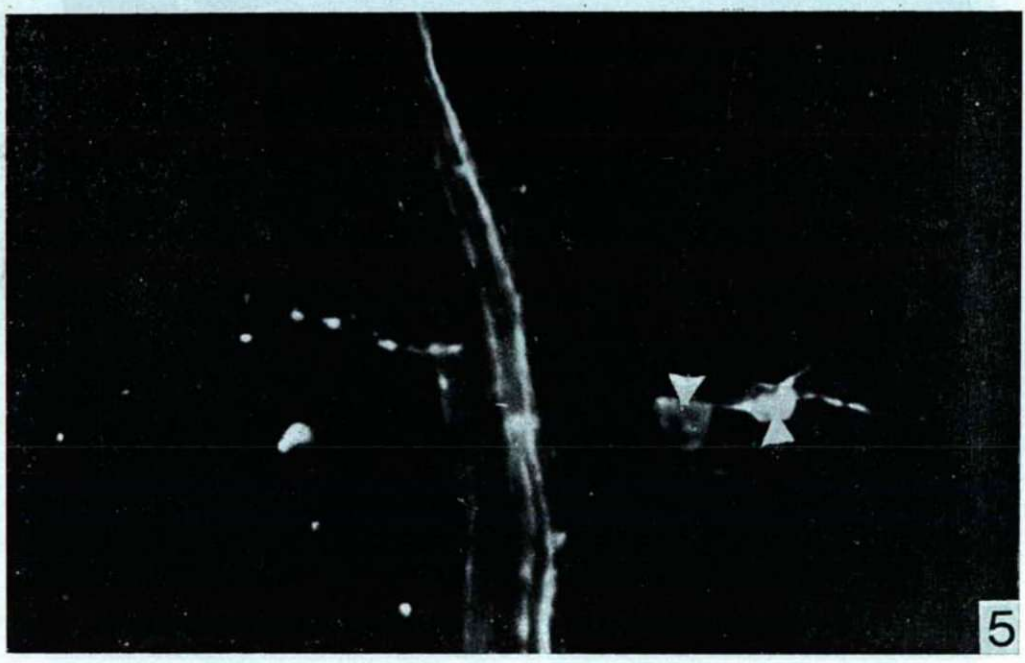
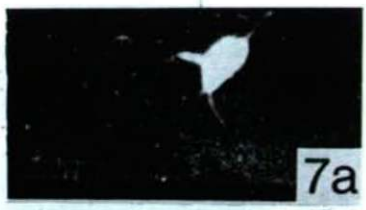


Fig. 4. Fluorescence induced by glyoxylic acid in the foregut of snail gastrointestinal tract. The thin varicose fibres (arrow) and the thick nerve bundles (arrow-heads) form a complicated network, at places with the small cells which are in close contact with the fibres (filled arroheads). ×580

Fig. 5. Fluorescent nerve bundle in the foregut. The thin varicose nerve fibre originating from the bundle as well as two neurons (filled arrow-heads) in the direct neighbourhood are observed. ×620



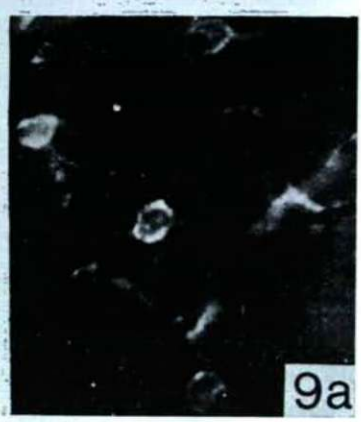


Fig. 6. and 7. Main types of neurons observed in the foregut wall. Most of the cells are multipolar, but bi- and unipolar types can also be found among them. The fluorescence is occasionally limited to the cytoplasm. ×620

Fig. 8. Fibres running in the hindgut wall. Varicosities (arrows) can well be seen in one part of the thinner fibres. ×620

Fig. 9. Detail of fluorescent nerve fibres found in the stomach wall. ×580

Fig. 9a. Groups of unipolar neurons can be seen at places among the fibres. In these the fluorescence is limited to the cytoplasm and its intensity is much lower than in the cells of the foregut. ×680

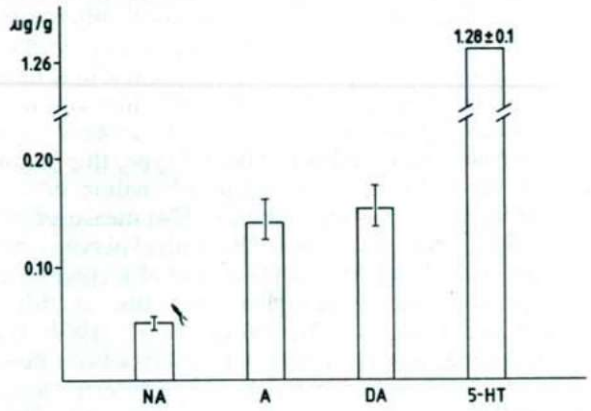


Fig. 10. Amount of monoamines in the snail gut expressed in µg/g wet weight.

III. Chemical studies

The snail gut contained monoamines in significant amount (Fig. 10). The 5-HT occurred in the largest number (1.25 µg/g wet weight), while the amount of noradrenaline was found to be lower by two orders (0.05 µg/g wet weight). The concentration of adrenaline and dopamine, was also significant (0.14 and 0.16 µg/g).

Discussion

The fluorescence microscopic studies have in many cases demonstrated the presence of monoamine (MA)-containing neurons in the central nervous system of snail (Dahl et al., 1966; Jaeger et al., 1970; Marsden and Kerkut, 1970; Sakharov and Zs-Nagy, 1968; Sedden et al., 1968). It is likely that in the central nervous system of the snail the dense-core vesicles are storing the MA, as this has been confirmed by several electronmicroscopic, electronhistochemical and autoradiographic experiments (Cottrell and Osborne, 1970; Gerschenfeld, 1963; Jourdan and Nicaise, 1970; Kuhlmann, 1970; Pentreath and Cottrell, 1973; Pentreath et al., 1973, 1974). The histochemical studies carried out on *Helix* (Cottrell and Osborne, 1969) and *Lymnaea* hearts (S.-Rózsa and Zs-Nagy, 1967) have demonstrated that MA-s are present both in the nerve and muscle elements. In the heart of *Aplysia* the localization of serotonin (5-HT) in nerve elements has also been verified by electronmicroscopic autoradiographic studies (Taxi and Gautron, 1969). On the basis of earlier and newer biochemical as well as physiological results it is presumable that MA-s function as neurotransmitters in the nervous system and heart of *Helix* (Gerschenfeld, 1973; Hiripi and Salánki, 1973; Juorio and Killick, 1972; Nemcsók et al., 1975; S-Rózsa, 1969; S-Rózsa and Perényi, 1966). Since large number of data prove the fact that the monoamines also act as mediators in the mammalian gut (Burnstock, 1983; Furness et al., 1980; Gabella, 1979; Komuro et al., 1982), the aim of our study was to attempt the demonstration of the presence of adrenaline, noradrenaline, dopamine and serotonin in the gut of *Helix pomatia*, as well as the probable neurotransmitter role of these in the regulation of the intestinal activity.

According to our results, each of the assumed monoamines were revealed in the snail gut. However, rather significant differences appeared in the concentration of the various monoamines. Serotonin was present in highest amount, noradrenaline could be demonstrated in the lowest concentration. The absolute amount of monoamines was rather low when comparing these values with the data measured in other molluscs. Since the tissue in question is of peripheral, visceral type, this is not surprising. Nevertheless, the ratio of serotonin, dopamine and adrenaline shows great similarity to the ratios measured in shells. SALÁNKI et al. (1974) measured 40 µg/g serotonin, 25 µg/g dopamine and 5 µg/g noradrenaline in the central nervous system of *Anodonta cygnea*. Adrenaline, noradrenaline and dopamine were also successfully demonstrated in the gut of animals phylogenetically of higher order, thus in fish, *Amphibia,* birds and mammals (EULER and FANGE, 1976; BRODIE et al., 1964; BOGDANSKI et al., 1963; MANUKHIN et al., 1969; NORTH, 1965). The results of our fluorescence microscopic studies — according to which, especially in the foregut, highly intensive and well localizable fluorescence could be detected both in the nerve fibres and in certain neurons — support by far the results of the chemical determination. In the possession of the data obtained with the two study methods, the statement can be regarded as grounded (HALASY and BENEDECZKY, 1983) that conformably to vertebrates, the monoamines play role as mediators in the gastrointestinal tract of snails as well. The fact that the majority of the fluorescent perikaryons were in close morphological contact with the fluorescent nerve fibres means that at least a part of the fluorescent fibres is intrinsic in origin. Nevertheless, the fact that cells having no visible morphological contact with fluorescent nerve fibres were also observed suggests that the other part of fluorescent fibres has extrinsic origin. This presumption is also supported by the data of the chemical measurements since in the snail gut the serotonin content was the highest, therefore it is probable that the large part of the separately fluorescent single cells may correspond to enterochromaffine cells of serotonin content. Naturally, it cannot either be ruled out that one part of the separately fluorescent cells are also neurons, however, in the processes the concentration of the monoamines was actually rather low — due to this the process system proving the neuron nature could not be indicated. Our electronmicroscopic results can also be well interpreted by the results of the chemical measurements and the fluorescence microscopic observations. First of all, what seems to be likely is that the terminals containing large dense-core vesicles found in the neighbourhood of the muscle fibres function with mediators of monoamine character. The circumstance that the large dense-core vesicles were not only found in the axon-terminals but also in the neuropils and in the perikaryon of certain neurons strengthens our earlier assumptions, namely that a rather developed local neuron network can be found in the snail gut similarly to the gut of vertebrates, the morphological features of which strongly resemble the Auerbach's plexus. However, while in the neuropil of the mammal myenteric plexus a large amount of mainly axo-axonic synapses were observed (KOMURO et al., 1982), so far synapses were hardly observed by us in the myenteric plexus of the snail gut. It seems that the morphological signs of the interrelationship between the neurons are less expressed in the snail gut compared to mammals. The neuromuscular junction itself, however, is essentially the same as in the vertebrates of higher order. Directly besides or somewhat further from the smooth muscle fibres, a large number of axon terminals filled with dense-core vesicles can be observed. They never establish synaptic contact with the sarcolemma, thus the possibility of fast stimulus-

transfer is not ensured. Since the cells in question are smooth muscle cells ensuring the peristaltic movement of the gut wall, this is not even necessary. It is probable that the mediator substances empty continuously into the extracellular space through exocytosis and their effect displays slowly but long-lastingly on the muscular tension. The classic determination of GERSCHENFELD (1973) according to which monoamines play significant role as neurotransmitters in the snail, is supplemented by our studies with the fact that the monoamines may also take part in the regulation of the function of the gastrointestinal tract, the physiological relations of which are to be clarified by further studies.

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ELECTRON MICROSCOPIC STUDY ON THE INNERVATION OF THE GUT-MUSCULATURE IN THE CARP *(CYPRINUS CARPIO)*

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Abstract

Authors studied the innervation of the muscles of the small intestine in lacustrian carp *(Cyprinus carpio)* with the help of electron microscopic method. Studies determined a complex myenteric plexus rich in nerve elements, found between the circular and longitudinal muscle layers. The myenteric plexus was made up of large, continuous neuropil areas, smaller fibre bundles penetrating the muscle layer and single axons. The occurrence of neurons hasn't been detected until now. Axon terminals were frequently found tightly close to the sarcolemma, however, the morphological signs of synaptic specialization were only occasionally observed. Dense-core vesicles with diameters of 60—100 nm were observed most frequently in the axon profiles. In their neighbourhood low amount of pleomorph agranular vesicles also occurred. Neurosecretory granules of varying electron density, with diameters of 200 nm were found in certain axon profiles. On the basis of their electronmicroscopic observations, authors assume that the simultaneous occurrence of aminergic — by the presence of the dense-core vesicles —, as well as peptidergic innervation — by the axon profiles containing neurosecretory granules — is very likely in the enteric nervous system of carp.
Key words: carp, gut musculature, innervation, electron microscopy.

Introduction

Recently interest has turned again towards the triple division (classification) of the autonomic nervous system proposed by LANGLEY in 1921, and within this the concept of the enteric nervous system (ENS).

Several authors (GERSHON et al., 1983; FURNESS et al., 1980) enumerate convincing evidences concerning the separation of the ENS. Each author emphasizes the diversity of the nerves of the ENS from morphological, chemical point of view, more exactly, in respect to their transmitter content. The descriptive studies on the fine structure of the ENS are mostly related to mammalian species (BAUMGARTEN et al., 1970; GUNN, 1968; KOMURO et al., 1982; WILSON et al., 1981), but recently similar studies have been performed in vertebrates of lower order, among them in a few fish species as well. BAUMGARTEN et al. (1973) demonstrated different monoamine-like transmitters in the gut of *Lampetra fluviatilis* with formaldehyde-induced fluorescence, and apart from this, they also gave fine structural description of the intestinal plexuses. Studying the nerve elements of the gut muscle in chondrostean fish, SALIMOVA and FEHÉR (1982) observed the presence of serotonin, dopamine and noradrenaline by histochemical and microspectrophotometric method and they also found nerve fibres of various type and different vesicle content by electron microscope. Histochemical data on teleosts are known on the basis of studies by BAUMGARTEN

(1967) on tench, and by WATSON (1979) on short-spined cottus, plaice and herring. The present paper reports on the results of ultrastructural studies on the enteric nervous system of the lacustrian carp, a teleost species which is general and has great economic significance in Hungary.

Materials and Methods

Studies were performed on mature male and female individuals of lacustrian carp *(Cyprinus carpio* L.*)*, obtained from the Fish-breeding Research Institute in Szarvas. The fish were stunned by blows, the abdominal cavity opened and 1 mm^3 pieces cut with razor blade from the midgut. The tissue samples were prefixed in cold state in 3% glutaraldehyde (pH 7.3) buffered with cacodylate for 4 hours. This was followed by 5 min. washing in cacodylate buffer containing 7.5% saccharose, and then the specimens were postfixed in the mixture of 4% osmium tetroxide: cacodylate buffer in the ratio 1:1 (pH 7.5) for 2 hours. In the course of dehydration in ascending alcohol series the material was contrasted for 30 min. in dark with saturated uranyl acetate dissolved in 75% alcohol. The samples were embedded in Durcupan ACM, and the prepared sections were postcontrasted with lead citrate. The sections were studied and photos were made on JEOL 100 B and TESLA BS 500 electronmicroscope.

Results

The rich plexuses of the nerve fibres of the small intestine in lacustrian carp were found in the connective tissue interstitium between the circular and longitudinal smooth muscle layers. The smooth muscle cells were rather irregular and had various shape. The cell nucleus relatively rarely fell to the plane of the section (Figs. 2 and 5). Both surface of the muscle cells and the cell nucleus were strongly indented. Variously wide, mostly indented intercellular spaces developed among the muscle cells (Figs. 1 and 2). Generally abundant collagen fibre substance could be observed in the intercellular spaces (Figs. 1 and 9), nevertheless, areas without fibres also occurred at places. At certain points the processes of the smooth muscles were found in close contact with each other (Figs. 3 and 6). The sarcoplasma was rich in myofilaments, but poor in mitochondria and other cell organelles. Depending on the plane of the section various amounts of so-called dense bodies (Z fragments) were striking due to their high electron density (Fig. 4). The marginal, myofilament-free parts of the sarcoplasma contained large amount of endocytotic vesicles (Figs. 2 and 4). Various amount of nerve fibre-cross sections were observable in the myenteric plexus among the smooth muscles (Figs. 1, 4). The nerve fibres were frequently covered by glial cell processes (Fig. 1), however, high amount of nerve fibres were also found without glial processes and the axolemmas were attached directly to each other (Figs. 1, 2 and 4). Large amount of parallelly-organized filament bundles occurred in the cytoplasm of some glial cell processes (Fig. 4). No transmitter-storing vesicles were found in the majority of the nerve fibres arranged in large bundles, however, varying amounts of agranular and granular vesicles were observable in the preterminal axons (Figs. 1, 2 and 4). Agranular vesicles were relatively few in the axon profiles, they occurred sporadically as independent (individual) axonprofiles, and were generally located in the neighbourhood of small and large dense-core vesicles. Their cross section was mostly pleomorph, their average diameter was 40 nm. Small and large dense-core vesicles were observed most frequently in the free axon terminals. The average diameter of these were 60 and 100 nm. The nerve fibres contained large

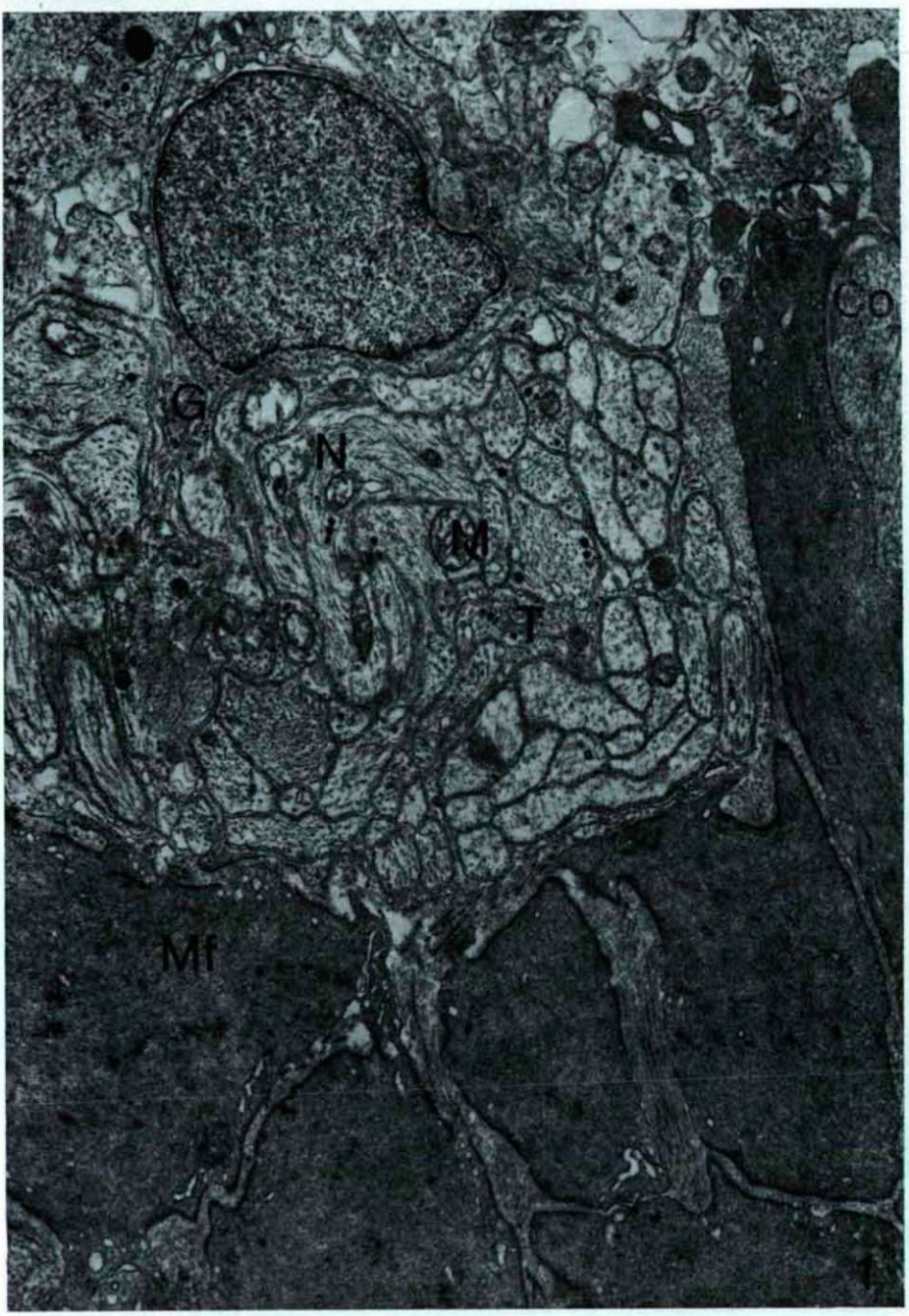

Fig. 1. Detail of myenteric plexus in the smooth muscle of carp gut. Mf = smooth muscle, N = axon profiles in the plexus, T = terminals, Co = collagen fibres, G = glial cell process, M = mitochondrium. ×15 000

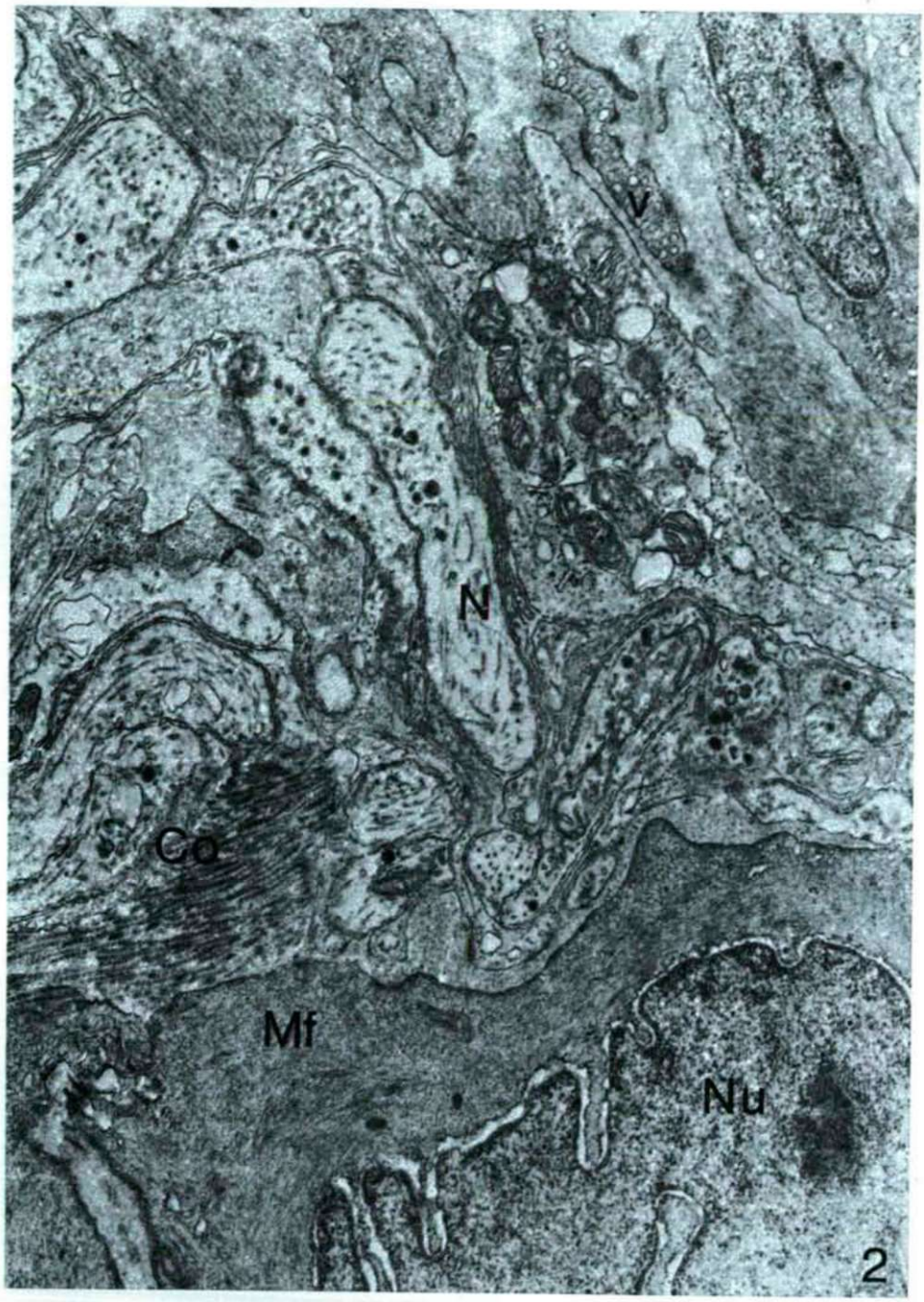

Fig. 2. Great amount of nerve elements (N) can be seen in the intercellular space rich in collagen (Co) between the smooth muscle cells (Mf) of carp gut. The nucleus (Nu) of the smooth muscle cells is of varying shape. Vesicles (v) referring to intensive endocytotic activity are observable on the sarcolemma. ×18 000

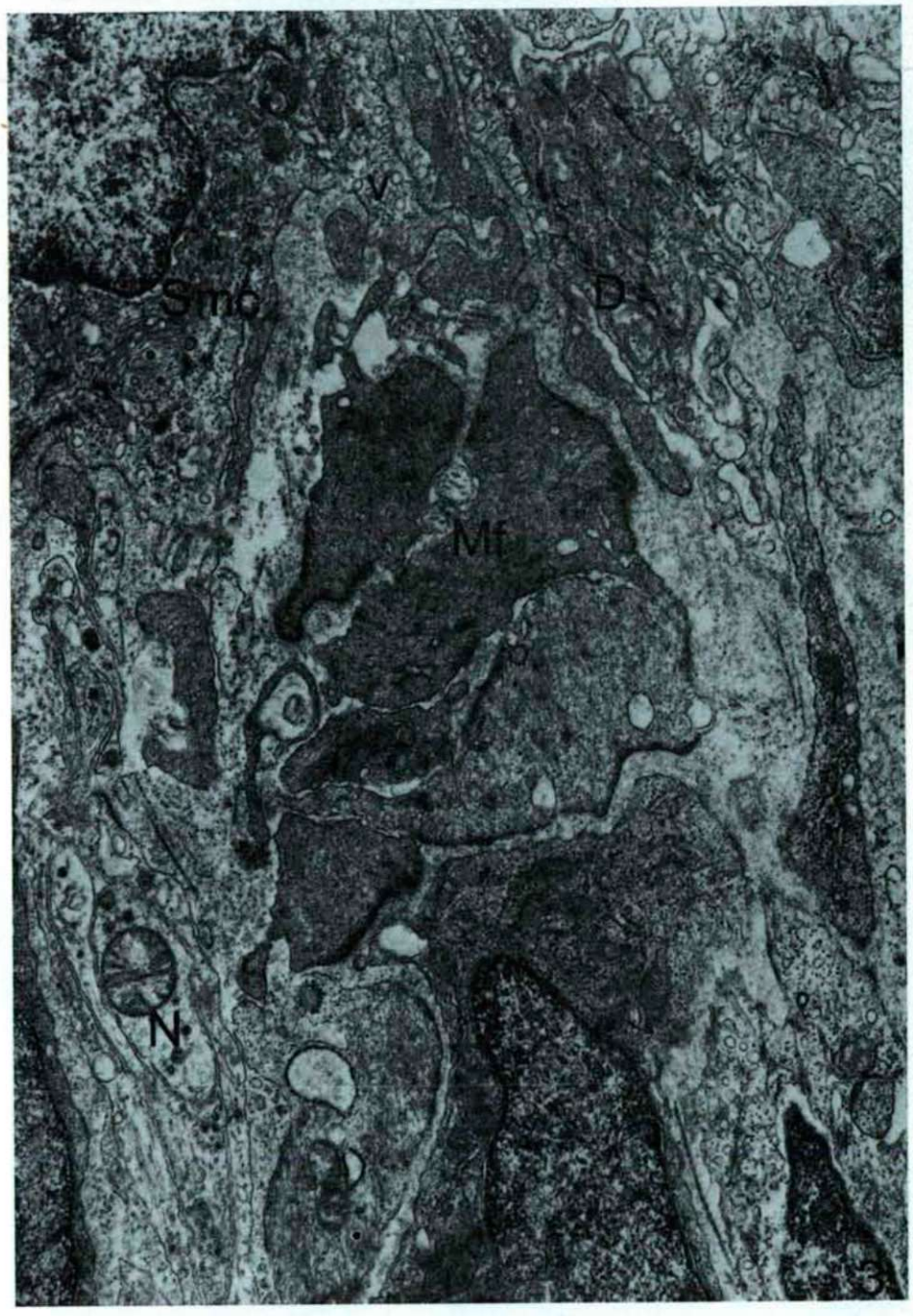

Fig. 3. Longitudinal nerve fibres (N) and cross-section of muscle cells originating from various depth: Mf = apical detail rich in myofilament, Smc = plane of intersection with nucleus rich in cell organelles. Rather large amount of endocytotic vesicles (v) can be seen in certain processes. D = desmosomes. ×18 000

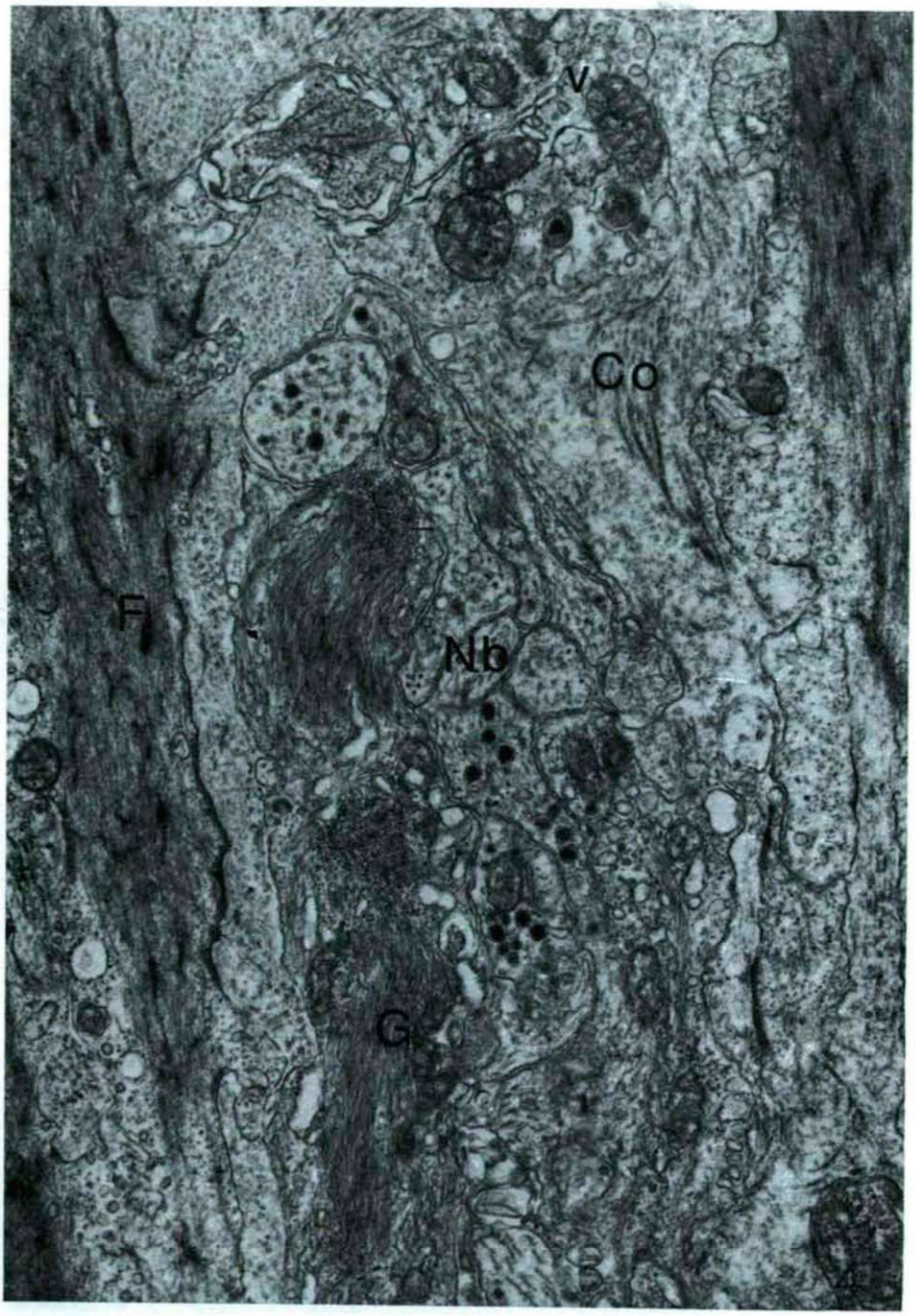

Fig. 4. Nerve bundle (Nb) in carp gut. Varying vesicle populations can be observed in certain axon profiles. The glial cell process (G) contains large number of filaments arranged in bundles. Co = collagen fibres, v = endocytotic vesicles, F = supporting sheath. ×18 000

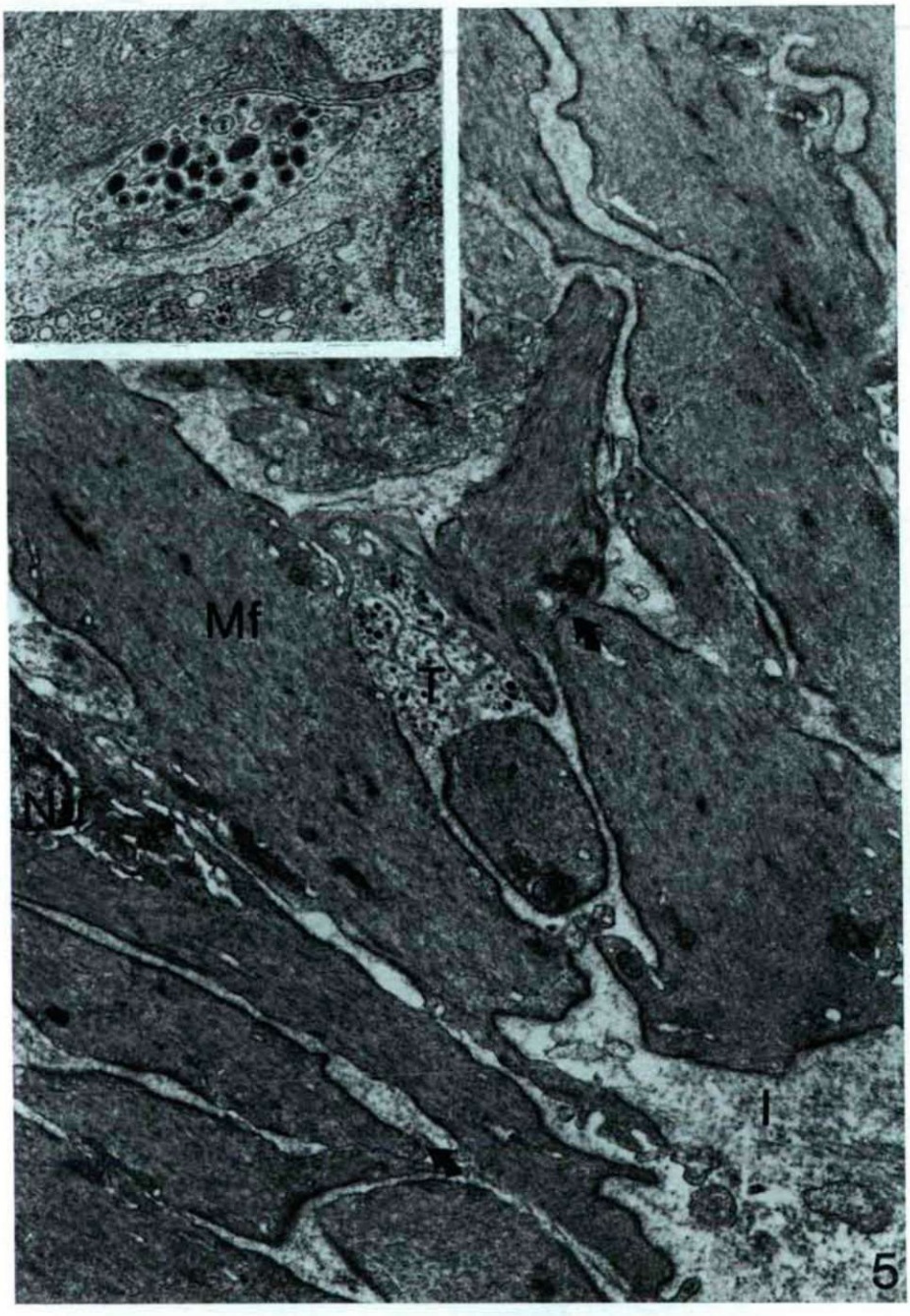

Fig. 5. Cross-section of axon profiles (T) in the direct neighbourhood of the muscle fibres (Mf). The arrow show the desmosome-like junctions of the smooth muscle cells. I = interstitium, Nu = nucleus. ×15 000
Insert: terminal, rich in dense-core vesicles at high magnification. ×40 000

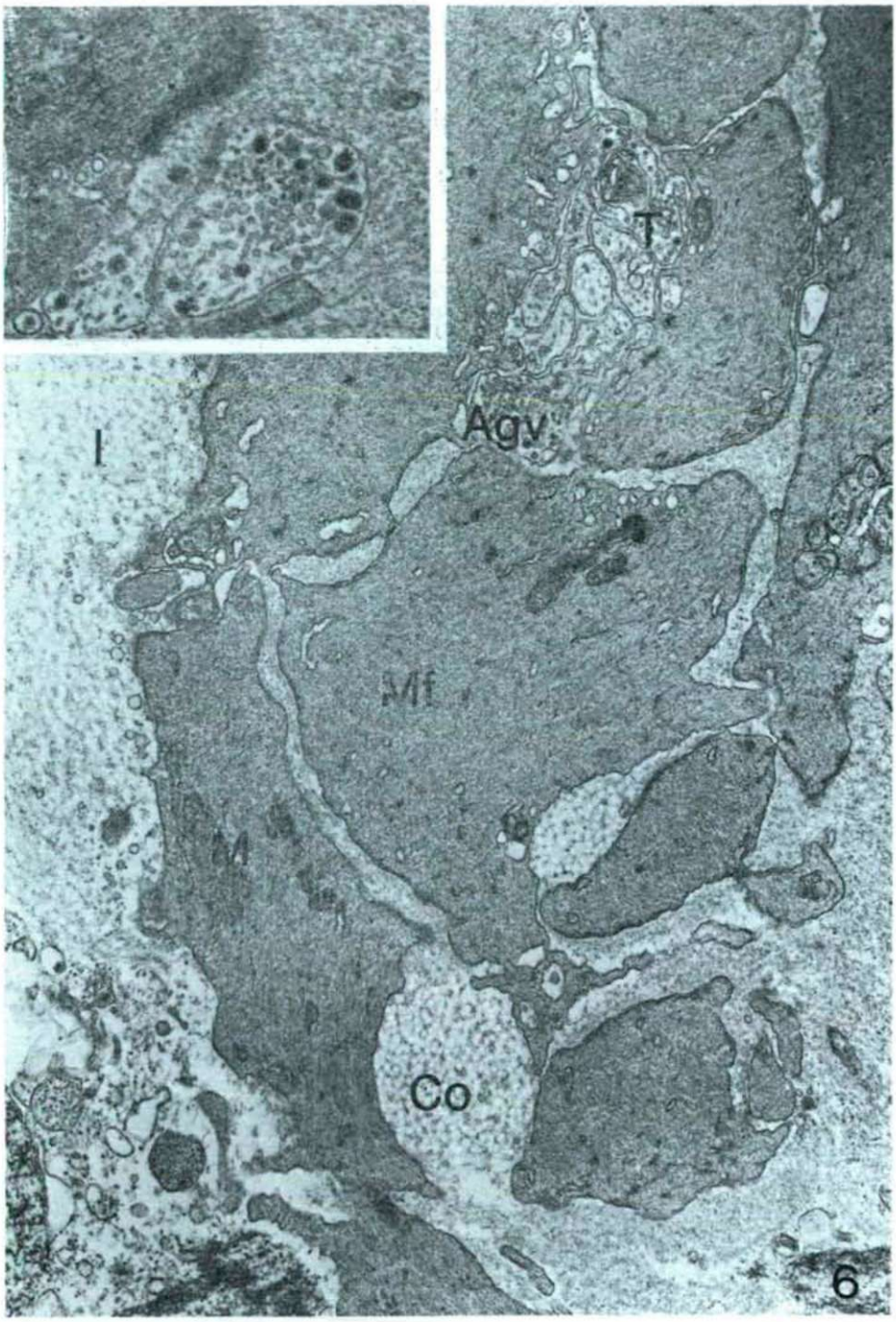

Fig. 6. Nerve fibres (T) in tight contact with the smooth muscle cells of the small intestine in carp. Mainly agranular vesicles (Agv) are situated in certain terminals. Mf = smooth muscle cell, I = interstitium, M = mitochondrium, Co = collagen fields. ×18 000
Insert: the above described terminal type at higher magnification. ×40 000

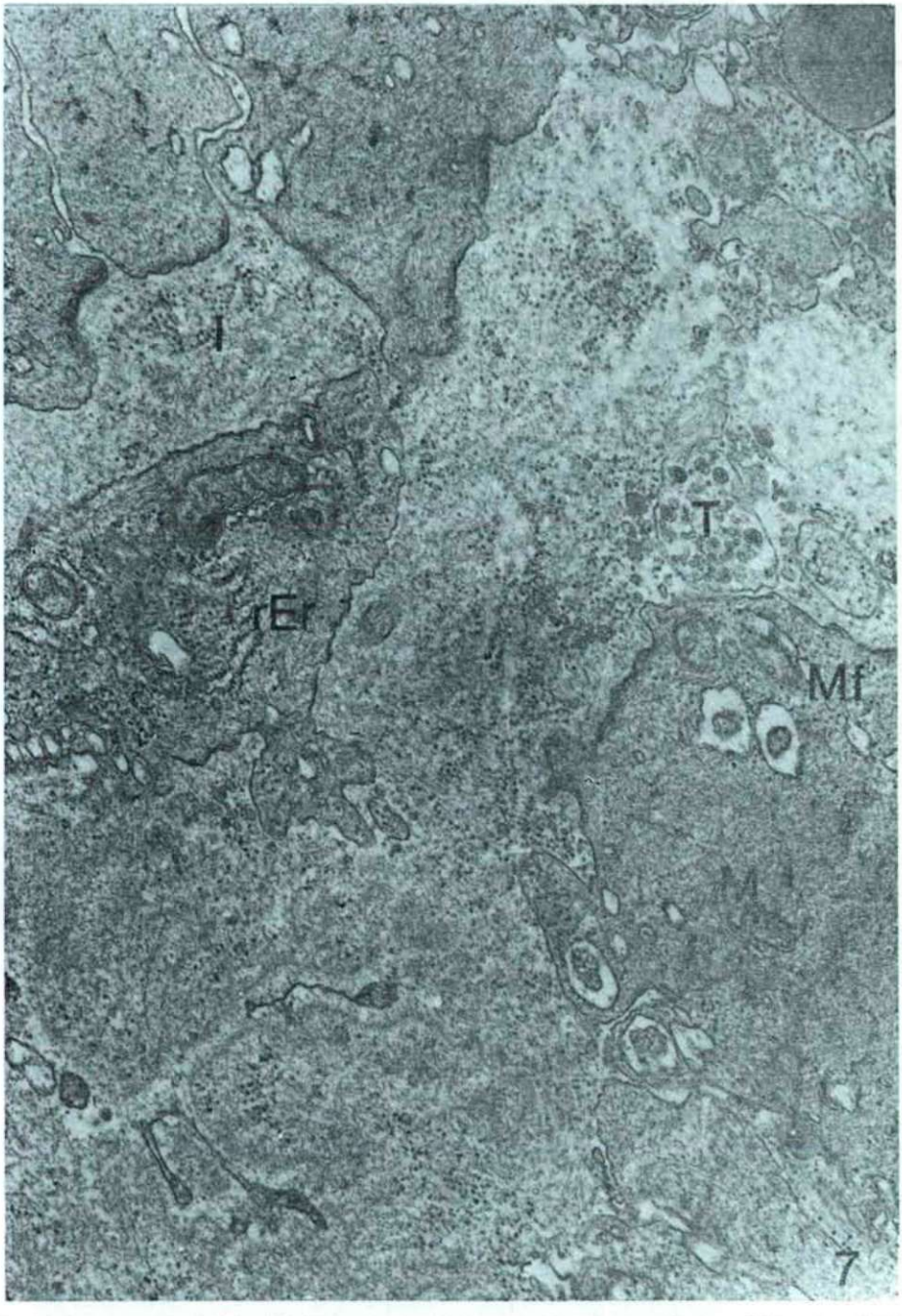

Fig. 7. Axon terminal (T) with dense-core and clear vesicles in the direct neighbourhood of a smooth muscle cell (Mf). The lack of glial covering is obvious on the surface of the axolemma. I=interstitium, rEr=rough surfaced endoplasmic reticulum cisternae, M=mitochondrium. ×25 000

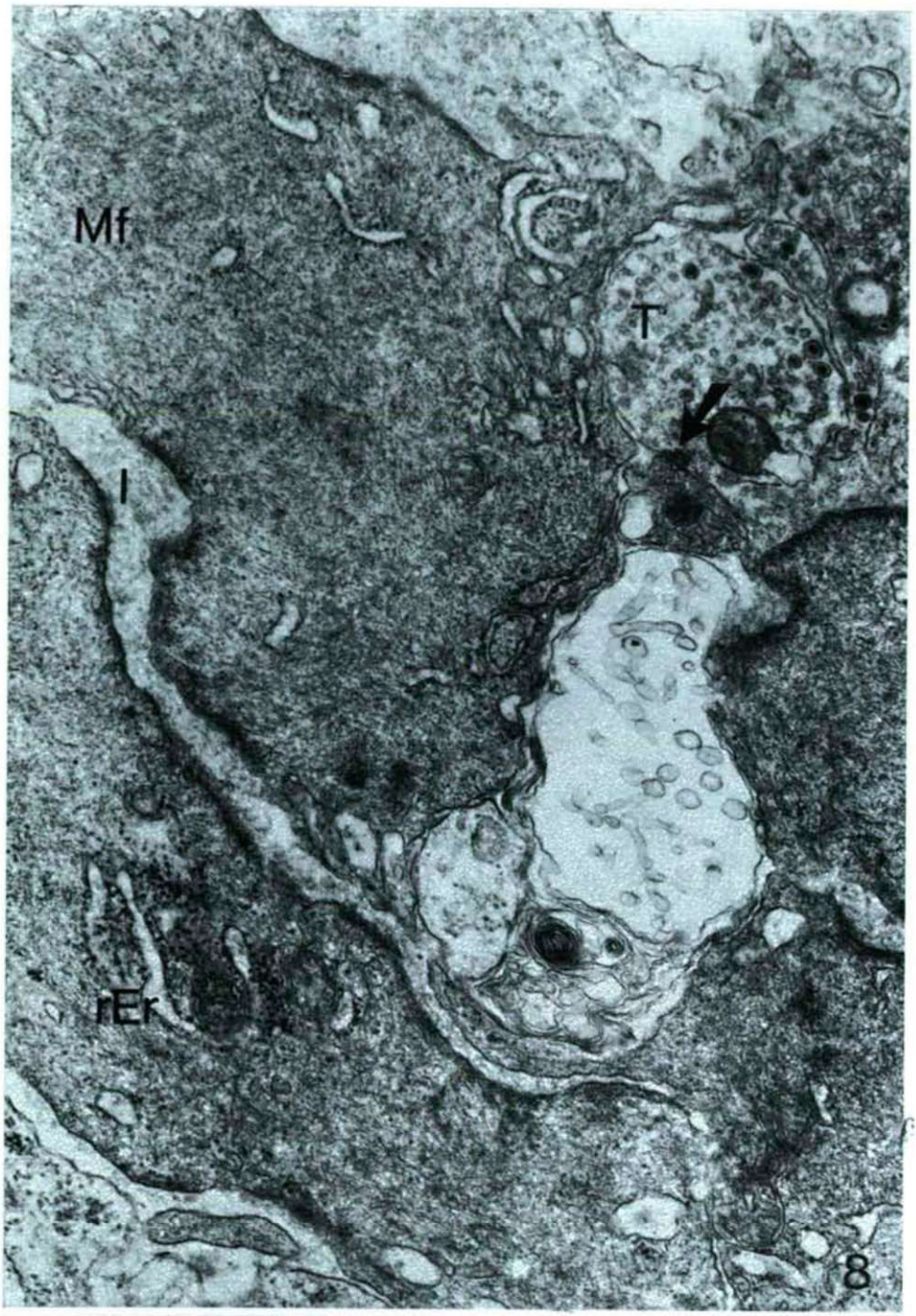

Fig. 8. The axon terminal (T) lying near the cell process of the smooth muscle contains granular and agranular vesicles. The presynaptic thickening refers to the synapse-like contact (arrow). Mf = smooth muscle, I = interstitium, rEr = rough surfaced endoplasmic reticulum. ×28 000

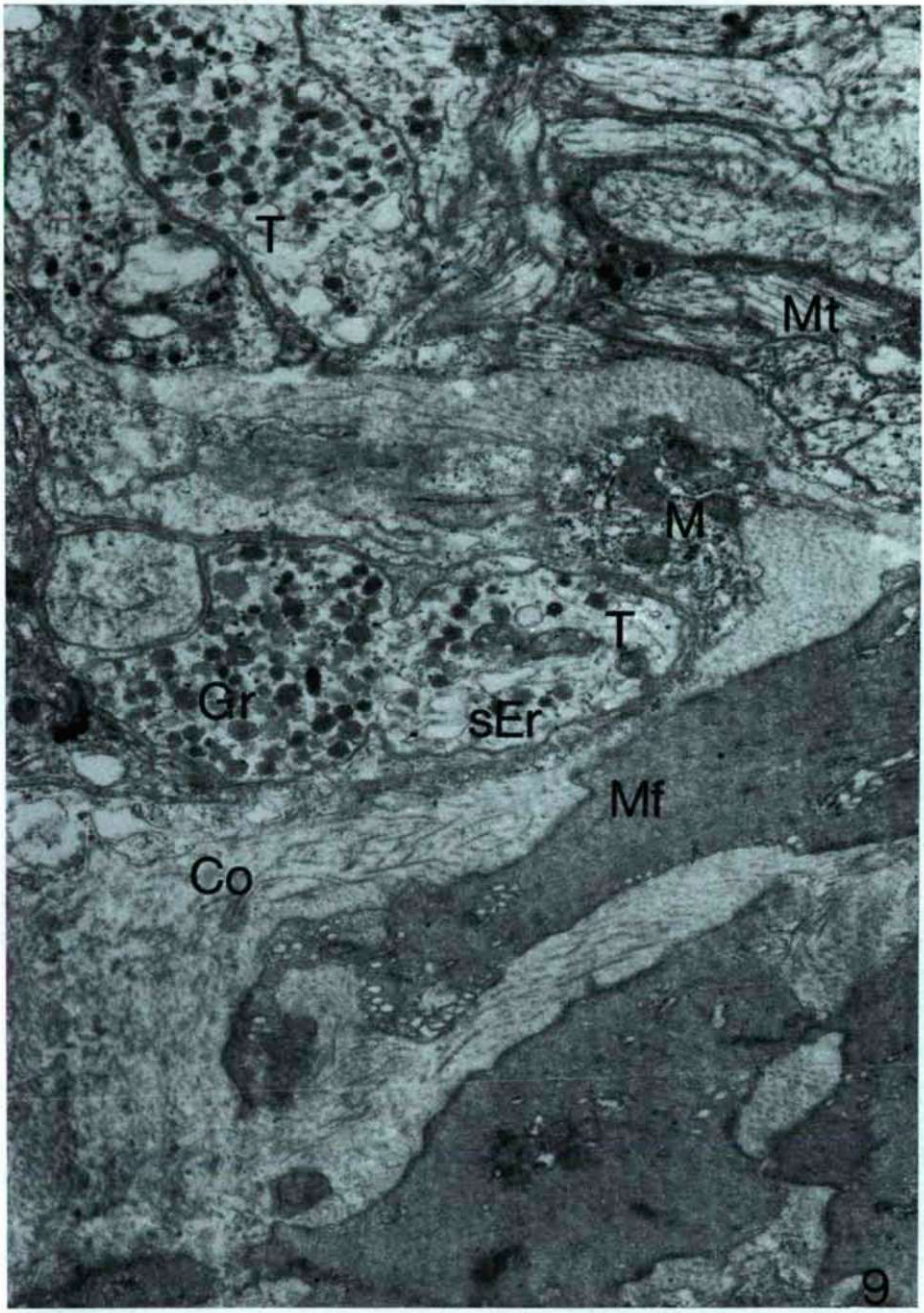

Fig. 9. Nerve fibres (T) filled with granules (Gr) of varying electron density are also found near the smooth muscle cells (Mf). Co = collagen fibres, M = mitochondrium, Mt = microtubuli, sEr = smooth surfaced endoplasmic reticulum. ×16 000

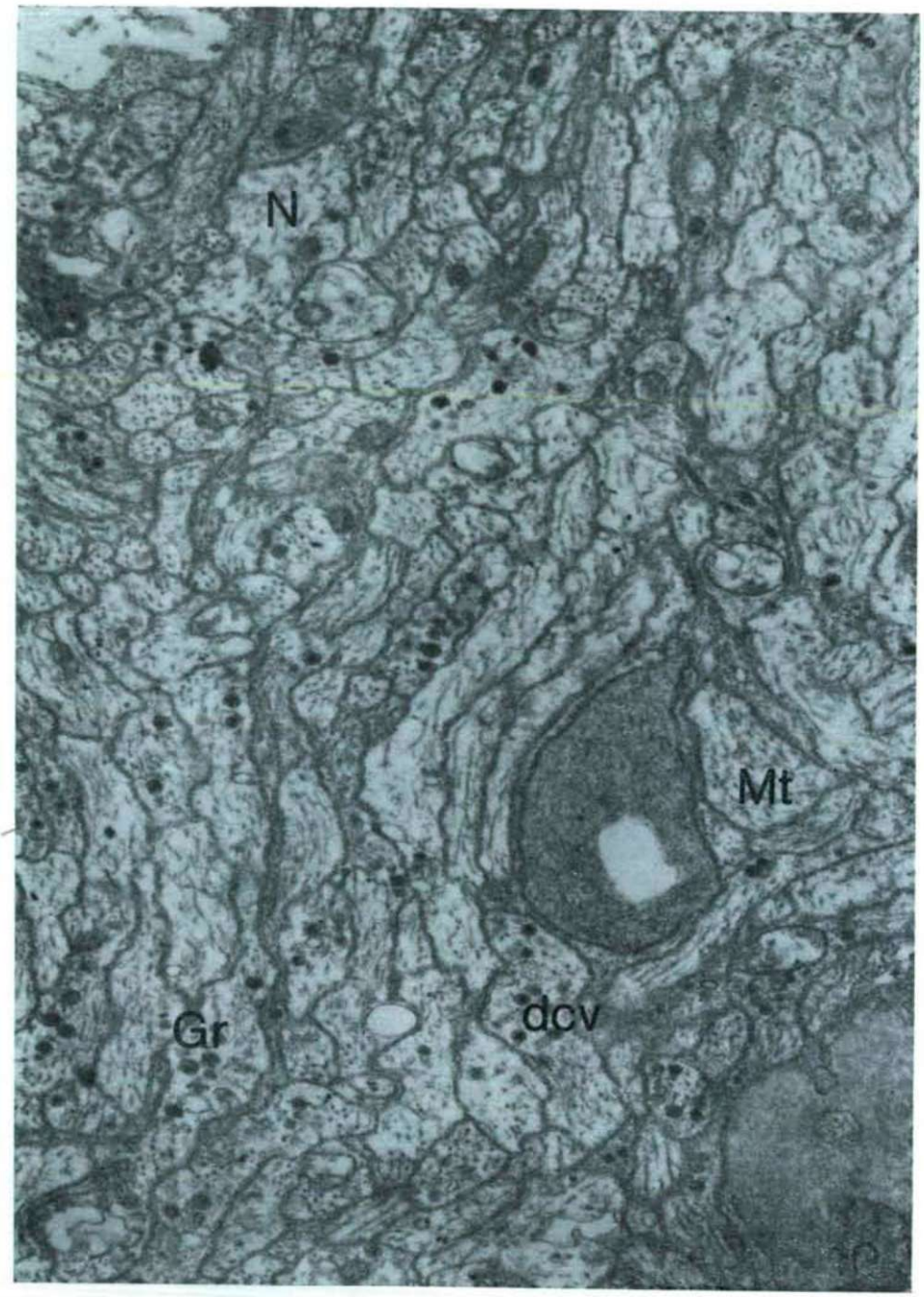

Fig. 10. Compact neuropil-detail from the myenteric plexus of carp. N = nerve fibre, Mt = microtubule, dcv = dense-core vesicles, Gr = neurosecretory granules. ×15 000

amount of microtubuli and neurofilaments. Synaptic junction was not observable despite the fact that the axolemma of certain axons of the nerve fibre bundles were frequently found in tight morphological contact.

In respect to the nerve-muscle relationship, the presence of a few (1—10) axon profiles was also often observed in the wide extracellular space of several muscle cells. Here, the membrane of several axons was found directly besides the sarcolemma of the smooth muscle. (Figs. 5 and 6).

Since in the majority of the axon profiles agranular and granular vesicles were present, it is presumable that the majority of these correspond to axon terminals (Figs. 5 and 7). Axon terminals with presynaptic membrane thickening and vesicle-accumulation referring to neuromuscular junction were very rarely observed (Fig. 8). Here, the postsynaptic membrane thickening of the sarcolemma was only of slight degree.

Apart from the axon types described so far, preterminal axons with granules of neurosecretory type were also seen at certain areas of the myenteric plexus (Fig. 9). The most obvious characteristic of these granules was the varying electron density: completely electron-lucent grains occurred besides rather electron dense ones. The large average diameter (200 nm) of the granules was also striking. The majority of the granules were rounded, some of them were of somewhat irregular shape. The limiting membrane was generally observable as a well distinguishable sharp line, seeming to be slightly indented at places. In this terminal vesicles of agranular type were only found in small number in the neighbourhood of the neurosecretory granules. Microtubule cross sections and a few smooth surfaced endoplasmic reticulum vacuoles were also found in the axon terminals apart from a few mitochondria. On the basis of their fine structural characteristics these granules presumably contain neuropeptides. These axon terminals which could be regarded as peptidergic, are rather close to the sarcolemma of the smooth muscle cells, however, their tight connection haven't been observed yet. Large, compact neuropil areas were frequently found in the myenteric plexus, in which rather various axon profiles were detectable (Fig. 10). The presence of microtubuli and microfilaments was striking in the majority of these profiles, but smaller-larger amounts of granules were also observed in some cases. The majority of these were dense-core vesicles, the smaller part was of neurosecretory type. Intercalary nerve terminals were not found in the extensive neuropil.

Discussion

Reviewing our neurohistological knowledge on the gastrointestinal system it can be determined that the innervation of the mammalian gut muscle is the most clarified (BAUMGARTEN et al., 1970; BURNSTOCK, 1983; FURNESS et al., 1980; GABELLA, 1979; GORDON—WEEKS, 1982; GUNN, 1968; KOMURO et al., 1982; WILSON et al., 1981). Relatively large amount of data are at disposal in respect to the gastrointestinal tract of insects (ANDERSON et al., 1977, 1978; BENEDECZKY et al., 1982) and certain molluscs, too (FRITSCH et al., 1977; HALASY et al., 1983; HEYER et al., 1973; MERCER et al., 1981). At the same time, fine structural data are rather rare regarding fish — representing an important developmental level in evolution.

All these justify the importance of studies carried out on fish. It is also surprising that light microscopic studies were mostly performed only from the beginning of the

century (BACKMAN, 1917; BOEKE, 1935; CHEVREL, 1893, 1894; LUTZ 1931; PATTERSON et al., 1933; STANNIUS, 1849). The reason for our electronmicroscopic studies was that detailed observations are already at disposal in respect to snail *(Helix pomatia)*, and insects, namely *Periplaneta americana* and *Locusta migratoria* (BENEDECZKY et al., 1982; HALASY et al., 1983). The aim was to clarify the innervation of the gastrointestinal tract of fish, being an important link in evolution.

From the results it seems worthy to emphasize that regarding the anatomical and fine structural features the most important characteristics in teleosts are very similar to those of mammals. It could be determined that the submucous plexus is still relatively undeveloped (WATSON, 1979), while the myenteric plexus is well developed. Both the circular and longitudinal muscle layers are richly innervated, smaller-larger amounts of nerve fibres or nerve bundles occur in almost every plane of section. It is also noteworthy that neurons cannot be found with such frequency as e.g. in the snail gut muscle, where aminergic as well as peptidergic cells can be found in high number (HALASY et al., 1983). This refers to the fact that the local neurons are not so significant as in invertebrates. It is also known that few giant cells of the neurosecretory type have mainly been found only in the hindgut of insect, (REINECKE et al., 1978). On the basis of studies performed on mammals so far (BURNSTOCK, 1983; GABELLA, 1979; KOMURO et al., 1982) it seems that at least 8—10 morphologically various types of nerve terminals can be found in the ENS. Regarding the histtochemical and fine structural studies carried out until now, it cannot be stated thathese 8—10 axon types represent the same number of neurotransmitters. At the same time the chemical, pharmacological and physiological studies (BURNSTOCK, 1983; FURNESS et al., 1980) make the role of at least 16 transmitter-candidates probable in the ENS as well. It must be certain that among the monoamines noradrenaline, dopamine and serotonin play role as mediators (BAUMGARTEN et al., 1970; FURNESS et al., 1980). The physiological role of acetylcholine is also rather unambiguously verified and newer data are also at disposal in respect to the occurrence of purinergic innervation (BURNSTOCK, 1983). A large number of mainly morphological and histochemical data supports the direct role of certain oligopeptides in the regulation of the intestinal activity; so far there are mainly morphological data on the substance-P, VIP, and the possible role of somatostatins and encephalines in mammals (BURNSTOCK, 1983). The estimation of these morphological observations is hindered by the circumstance that the regular physiological and pharmacological study of above peptides has not been performed yet. Accordingly, there is a lack in those most important physiological criteria on the basis of which the peptidergic regulation could be regarded to be proved. Our own studies on fish also seem to verify the considerations presuming multifactoral nerve regulation in mammals. The various types of vesicles were also found by us in the axon terminals of the fish gut muscle (agranular and granular, peptidergic). The role of aminnergic innervation has been supported by many authors, mainly with fluorescence, chromatographic and other studies (BAUMGARTEN, 1967; BAUMGARTEN et al., 1973; SALIMOVA et al., 1982; SANTER, 1977; WATSON, 1979). During the course of our biochemical studies under progress, so far we have been demonstrated the presence of noradrenaline, adrenaline and dopamine in the gut of carp (NEMCSÓK et al., unpublished data). On the basis of these chemical measurements as well as on the above mentioned literary data it can be unambiguously determined that each of the listed biogenic monoamines may play role as neurotransmitter or neurohormone in the gut muscle. It is more difficult

to judge the role of the neuropeptides. Even histochemical studies have only occasionally been performed in this field. On the basis of the results obtained on insects (BROWN, 1975; STARRAT et al., 1980) and mammals (BURNSTOCK, 1983; FURNESS et al., 1980) so far, furthermore, concerning the occurrence of peptidergic axon profiles found by us in lacustrian carp, it is likely that the neuropeptides may influence the function of the intestinal muscles in fish as well.

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CEROPALIDAE FROM SRI LANKA (HYMENOPTERA)

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Abstract

Taxonomic notes are presented on four species of Ceylonese *Ceropalidae* belonging to the genera *Ceropales* LATREILLE, *Bifidoceropales* PRIESNER, and *Irenangulus* SCHULZ, partly published by CAMERON (1897, 1900) partly collected by K. V. KROMBEIN as well as by members of the National Museum in Sri Lanka. The female of *Bifidoceropales declivis* (HAUPT) was not known and this species is new to the Oriental fauna.

Key words: Hymenoptera, Ceropalidae, taxonomy, Sri Lanka.

Introduction

All records of *Ceropalidae* species were published from Sri Lanka by CAMERON (1897, 1900) as *Ceropales albovariegata, C. albomaculata* and *C. parva.*

During the investigations of K. V. KROMBEIN in Sri Lanka, there were collected 75 specimens (54 ♀ and 21 ♂) which represent 2 further Ceropalids species new to Sri Lanka: *C. ligea* BINGHAM and *Bifidoceropales declivis* (HAUPT). It is quite possible that some taxa described from India or from Burma may be collected in Sri Lanka eventually.

I am much obliged to K. V. KROMBEIN for the dispatch of the Ceylonese material as well as to M. C. DAY (British Museum, Natural History, London), to P. I. PERSSON (Swedish Museum of Natural History, Stockholm) and to G. C. VARLEY—M. J. SCOBLE (Hope Department of Oxford) for the loan of some of Bingham's, Haupt's and Cameron's type-material for a revision, and to E. C. DAHMS (Queensland Museum, Brisbane), to L. MASNER (Biosystematics Research Institute, Ottawa), to J. PAPP (Zoological Department of Hungarian Natural History Museum, Budapest) and to R. WAHIS (Chaudfontaine, Belgium) for submitting material.

Results

Irenangulus albovariegatus CAMERON, 1897

Ceropales albovariegata CAMERON 1897 Mem. Proc. Manchr lit. phil. Soc. *41 (4):* 84 ♂.
Ceropales albovariegata: 1897, BINGHAM, Fauna Brit. India, Ceylon, Burma *1*: 176 ♂.
Xanthampulex albovariegata: 1912, TURNER, Ann. Mag. nat. Hist. (Ser. 8) *10:* 362.
Hypsiceraeus albovariegatus: 1915, CAMERON, Trans. ent. Soc. London: 405.
Xanthampulex albovariegata: 1917, TURNER, Ann. Mag. nat. Hist. *20:* 359.

Specimen examined: "Mussoorie, Rothney", "*Ceropales albomaculatus* CAM. type", "*Irenangulus* ♀ *albovariegatus* CAM. R. WAHIS dt. 77" 1 ♀. Type-specimen, originating from INDIA Uttar Pradesh), deposited in Oxford.

The holotype of the *Ceropales albovariegata* CAMERON was recorded from "Trincomali, CEYLON (Yerbury)", deposited? According to Wahis's synonymy, *C. albovariegata* CAMERON must be transferred to the genus *Irenangulus*.

Ceropales parva CAMERON, 1900

Ceropales parva CAMERON, 1900, Ann. Mag. nat. Hist. *5:* 20 ♂.

This species, reported from "CEYLON (Yerbury)", of very small size (only 4 mm), with abdomen and legs rufous, thorax black except the pronotum and propleurae with light spots probably distinguishable from the other *Ceropales* species, but lack of diagnosis on the form of the frons, propodeum and claws the generic relegation among the *Ceropalidae* can not be decided.

Ceropales ligea BINGHAM, 1903

Ceropales ligea BINGHAM, 1903, Fasc. malayenses I: Appendix V ♀
Ceropales ligea: 1906, BINGHAM, Fasc. malayenses III: 41, Plate A figs 4, 4a—4c ♀
Ceropales ligea: 1910, TURNER, Proc. zool. Soc. Lond.: 339 ♀ ♂
Ceropales ligea: 1934, BANKS, Proc. Am. Acad. Arts Sci. *69:* 114

Specimens examined: 59 ♀ and 19 ♂: MALAYSIA: "Sungkei 11/2/02", "ANNANDALE & ROBINSON, Siamese Malay States 1903—127", "*Ceropales ligea* BINGH. ♀ Type", "Type" (round label with red margin), "B. M. Type Hym. 19.772" 1 ♀ (London)*. — BURMA: TENASSERIM SHWEGYIN 7.89 Col. BINGHAM 1 ♀ (London). — SRI LANKA: 47 ♀, 17 ♂: *Northern Province.* Mannar District: 4 ♀, 1 ♂, Cashew Corp. Ma Villu, 17—21 Feb, 16—19 Sep (in Malaise trap), K. V. KROMBEIN, T. WIJESINHE, S. SIRIWARDANE, A., T. and V. GUNAWARDANE, P. B. KARUNARATNE, L. JAYAWICKREMA (Washington**, Budapest); 2 ♀ Kokmotte Bungalow 5 mi NE Wilpattu Natl Park, 21—25 May, K. V. KROMBEIN, P. B. KARUNARATNE, S. KARUNA, D. W. BALASOORIYA, G. RATNAVIRA, T. WIJESINHE, M. JAYAWEERA (Washington); 1 ♀ 2 ♂, Kondachchi, Silavathurai and Ma villu, 23—27 Jan, 11—12 Apr, K. V. KROMBEIN, L. WEERATUNGE, P. LEANAGA (Washington, Budapest). *North Central Province.* Anuradhapura District: 1 ♀ Wildlife Soc. Bungalow Hunuwilagama, Wilpattu 200 ft, 10—19 Mar. DAVIS & ROWE (Washington); 1 ♀ Padaviya 180 ft 19 Mar (light trap), P. B. and S. KARUNARATNE, D. W. BALASOORIYA (Washington); 1 ♀ the same locality and collector, 12—22 Mar (Washington). *North Western Province.* Puttalam District: 2 ♀, Wilpattu Natl Park, Kali Villu and Mullikulara Modaragam Aru, 12—14 Jun, D. H. MESSERSMITH, G. L. WILLIAMS, P. B. KARUNARATNE (Washington, Budapest); 1 ♂ Wilpattu Natl Park, Mullikulara Modaragam Aru 13 Jun, collected as before (Washington). *Eastern Province.* Amparai District: 9 ♀, 3 ♂, Ekgal Aru Reservoir Jungle 100 mts (partly in Malaise trap) and Ekgal Aru Tank, 19—22 Feb, 9—11 Mar, 9—12 Jun, 4—7 Jul, 11—15 Sep, K. V. KROMBEIN, P. B. KARUNARATNE, T. WIJESINHE, V. KULASEKARE,

* London = British Museum (Natural History, Department of Entomology, England
** Washington = National Museum of Natural History, Smithsonian Institution, Washington, U.S.A.

L. JAYAWICKREMA, M. JAYAWEERA, S. SIRIWARDANE, P. FERNANDO, D. W. BALASOORIYA, S. KARUNA (Washington, Budapest); 1 ♀ Lakugala Sanctuary (in Malaise trap), 13 Jun, K. V. KROMBEIN, P. B. KARUNARATNE, S. KARUNA (Washington). Trincomalee District: 1 ♀ Trincomalee, China Bay Ridge Bungalow 0—100' 13—17 May, K. V. KROMBEIN, P. B. KARUNARATNE, S. KARUNA, D. W. BALASOORIYA (Washington). *Central Province.* Kandy District: 5 ♀, 3 ♂, Udawattakele Sanctuary 2100 ft, 16—31 Aug, S. KARUNA (Washington, Budapest). Matale District: 1 ♀, 1 ♂, Kibissa 0.5 mi West of Sigiriya jungle 28 Jun—4 Jul, K. V. KROMBEIN, P. B. KARUNARATNE, T. WIJESINHE, V. KULASEKARE (Washington); 3 ♀ Sigiriya jungle, 28 Jun—4 Jul (in Malaise trap), K. V. KROMBEIN, T. WIJESINHE, V. KULASEKARE, D. H. MESSERSMITH, G. L. WILLIAMS, P. B. KARUNARATNE (Washington, Budapest). *Sabaragamuwa Province.* Ratnapura District: 1 ♂ Uggalkaltota, 23—26 Jun (in Malaise trap), K. V. KROMBEIN, P. B. and N. KARUNARATNE, T. WIJESINHE, L. JAYAWICKREMA (Budapest). *Uva Province.* Badulla District: 4 ♀, Ulhitiya Oya, 15 mi NNE of Mahiyangana, 5—6 Sep, K. V. KROMBEIN, P. B. KARUNARATNE, T. WIJESINHE, L. JAYAWICKREMA, V. GUNAWARDANE (Washington, Budapest). *Southern Province.* Monoragala District: 11 ♀, 4 ♂, Angunakolapelessa 100 mts 21—23 Jan, 27—28 Mar, 17—19 June, 30 Sep—1 Oct, 8—9 Oct (in Malaise trap), K. V. KROMBEIN, T. WIJESINHE, L. WEERATUNGE, S. SIRIWARDANE, T. and V. GUNAWARDANE, P. B. KARUNARATNE (Washington, Budapest); 1 ♂, Mau Ara 100 m 10 mi E of Udawalawa, K. V. KROMBEIN, P. B. KARUNARATNE, T. WIJESINHE, M. JAYAWEERA (Washington). — INDIA: 1 ♀, Dohnavur, 8 Oct, Tinnevelly Dt. (Budapest); 1 ♂, Deesa, Dec, (London); 1 ♀ Walayar Forests, S. Malabar, S. India, Jul, Nathan (Ottawa); 1 ♀, Anamalai Hills, Cinchona, May, Nathan (Ottawa); 1 ♀, Mysore Nandy Hills, 1200 m, 15 Apr, T. S. THOMAS (coll. Wahis). — INDONESIA: *West Java:* 10, Guning Malang 3—4000 ft, Nov, K. M. WALS (Budapest). — THE PHILIPPINES: 1 ♂ Cuernos Mt. Negros, BAKER (Budapest). — AUSTRALIA: 1 ♀, Mackay, Jan (London); 1 ♀, Alexandria, N. Austr. W. STALKER (London); 3 ♀, Brisbane, Indooroopilly, Quensland, I. D. GALLOWAY (London, Budapest) and 1 ♀ Brisbane, 17 Jan, H. HACHER, (Brisbane).

According to Bingham's diagnosis "In a collection of Burmese Hymenoptera there are two females of this species". The locality data of the first specimen correspond to the original diagnosis and it was supplied with the type-inscription and a separate type-label, consequently this specimen can be regarded as the holotype. The second specimen of the original material was published by TURNER (1910) with the locality Burma (♀), together with a specimen from Mackay, Australia. At the same time TURNER shortly described also the male of this species. Bingham's diagnosis and Turner's description can be supplemented as follows:

♀♂. Frons remarkably flat just before antennal sockets and broken in an obtuse angle at its two-thirds length between fore ocellus and antennae. Propodeum conspicuously flat along its whole length viewed from the side, surface finely granulated with a remarkably narrow and rather deep longitudinal furrow basally not reaching the middle of the segment. Both claws of fore and middle tarsi normal, with a short erect and acute subapical tooth, not bifid. Both claws of the hind tarsus rectangularly curved.

♀. — Lenght 5—7.5 mm. The colouring is variable. Holotype with the spots on front of all coxae becoming gradually smaller backwards; the interrupted white line on abdominal segments 4 developed only on the species from Burma, mandibles

with a very small white spot, first antennal joints brownish red in front. Neither the colouring of tergite 4, nor the same of the fore and the middle tarsi as well as of the inner spur (=carcaria) on the hind legs are uniform. Two specimens from Brisbane with larger black spots on clypeus, but with a smaller and shorter white streak on tergites. Among the 45 females originating mostly from Sri Lanka there are 12 with nearly entirely black tergite 4, while 33 specimens with a narrow curved band on each side of apical margin. Tarsal joints of middle legs dark only on 12 specimens, while 33 specimens are like the fore tarsal joints. Inner spurs of hind legs brownish only on 9 specimens (as in holotype) and white on 36 specimens. Mandibles entirely yellow only on the lighter coloured specimens and only partly on the darker specimens.

♂. — 3.5—5.5 mm. On the basis of 1 male specimen TURNER had published the head being entirely black, the clypeus and labrum fuscous, the scape alone marked with white beneath. Among the 17 males collected in Sri Lanka there are only 2 males with brown labrum and with black clypeus except the two light triangular spots on the lateral corners. 14 male specimens have a narrow longitudinal black spot on the light clypeus and on labrum except of one transitional variation with a broader longitudinal black spot on clypeus. However, the colouring of the head on the 17 males similar fo females, namely the subantennal and the supraclypeal area connected with the spot in emargination of eyes; a narrow line behind eyes ivory white except sometimes the black genae below. The spurs of the hind tibiae black only on 4 males and the inner one white on 12 males. The hind femora reddish dark brown on one specimen from India and not red as on specimens from Sri Lanka. The colour variation of this species seems to be rather large.

Distribution. MALAYSIA (BINGHAM, 1903). BURMA, QUEENSLAND, AUSTRALIA (TURNER, 1910) THE PHILIPPINES (BANKS, 1934) and SRI LANKA, INDIA, INDONESIA (West Java).

Bifidoceropales declivis (HAUPT, 1934)

Ceropales declivis HAUPT, 1934, Ark. Zool. *27A:* 11 ♂
Ceropales declivis HAUPT, 1938, Ark. Zool. *30A:* 10 ♂

Specimens examined: 7 ♀, 7 ♂: CHINA: 1 ♂ holotype, "Kina N. O. Szechuan", "Sven Hedins Exp. Ctr. Asien DR. HUMMEL", "1/6", "Holotype" red label, "*declivis* HPT. det. HAUPT, 1933" with Haupt's writing (Stockholm). — SRI LANKA: 7 ♀, 4 ♂: *Northern Province.* Mannar District: 2 ♀, Kondachchi, Ma Villu, 19 Sep (in Malaise trap), T. WIJESINHE, L. JAYAWICHREMA, V. GUNAWARDANE (Washington). *North Central Province.* Anuradhapura District: 1 ♀ Hunuvilagama, near Wilpatu, 200 feet (in Malaise trap), 28 Oct—3 Nov, G. F. HEVEL, R. E. DIETZ, S. KARUNARATNE, D. W. BALASOORIYA; 1 ♀ Ritigala Nat. Reserve 19. Sept. K. V. KROMBEIN, P. B. KARUNARATNE, T. WIJESINHE, L. JAYAWICKREMA, V. GUNAWARDANE (Budapest). *Eastern Province.* Trincomalee District: 3 ♂ China Bay Ridge Bungalow, 0—100', 13—17 May (in Malaise trap), K. V. KROMBEIN, P. B. KARUNARATNE, D. W. BALASOORIYA (Washington, Budapest); 1 ♀ China Bay Ridge Bungalow, 0—50 feet, 24—25 Jul (in Malaise trap), K. V. KROMBEIN, T. WIJESINHE, V. KULASEKANE, L. JAYAWICKREMA (Washington). *Central Province.* Matale District: 1 ♂ Kibissa, 0.5 mi West to Sigiriya, jungle, 28 Jun—4 Jul (in Malaise trap), K. V. KROMBEIN, P. B. KARUNARATNE, T. WIJESINHE, V. KULASEKARE. *Southern*

Province. Monoragala District; 1 ♀ Angunakolapelessa 27—28 Mar (in Malaise trap), K. V. KROMBEIN, T. WIJESINHE, L. WEERATUNGE (Washington); 1 ♀ Mau Ara 100 m. 10 mi E of Udawa lawa, 24—26 Sep (in Malaise trap), K. V. KROMBEIN, P. B. KARUNARATNE, T. WIJESINHE, M. JAYAWEERA (Budapest). — SOUTH INDIA: 1 ♂ Walayar Forests, S. Malabar, Sep, P. S. NATHAN (Ottawa). — TAIWAN: 1 ♂ Takao, May, SAUTER (coll. Wahis).

Haupt's description can be supplemented as follows.

♂. — Length 6.5—7 mm. The green tint given by HAUPT is very faint, the light parts more ivory white or sometimes (Taiwan, S. India) partly very finely yellowish. Tergite 6 not always entirely ivory white, but often with only a small line light apically and broadly interrupted medially, similarly to the previous tergites. Basis of mandible black and with a large white spot only on one male (Sri Lanka). The light inner eye margin usually continuous or interrupted on 3 males from Sri Lanka and on one male from India. The light spots of legs larger on four specimens (Sri Lanka) than on holotype. Trochanter largely black, but with a narrow light streak apically (as also on holotype); middle tarsus red (except holotype), only the hind one blackish. Wing hardly infuscated; upper margin of radial cell 3 shorter than 2 (on holotype, on each male from Sri Lanka and India), but at least as long as the same vein of 2 on the other specimens. Basis of the propodeum more or less finely rugulose on both sides of the triangular incision. Frons, propodeum and claws see later.

♀. — Length 4.7—6 mm. Similar to male, differing as follows: ivory white spots in emargination of eye ending sharply before antennal sockets; lower face above clypeus largely black, ivory white only laterally, sometimes fusing into a continuous streak with the small spot medially (lower face on male ivory white except a very small black spot just between the antennal sockets). Scutellum often black without a light spot. Hind coxa largely black at basis and only moderately ivory white on its apical third. Tergite 6 ivory white. Sculpture of head, thorax as in male, only the acute triangular incision of propodeum basally narrower and deeper. Last sternite triangular and acute.

This species very similar to *Ceropales ligea* BINGHAM, especially in colour. While legs of *declivis* (HAUPT) largely red, those of *ligea* largely black except mainly the hind red femora. These further additions to the known descriptions (♂♀) contribute to separate the two species. Frons convex in lateral view and not broken in an obtuse angle on its three-quarters length between fore ocellus and antennae; frons, pronotum, mesonotum with rather dense erect hairs; propodeum moderately convex basally and flattened on its distal two-thirds viewed from the side. Both claws of fore (♀) and middle (♀♂) tarsi bifid, with a long appressed, obliquely truncate subapical tooth; inner claw of fore leg (♂) very deeply split owing to the unusually large, not truncate inner tooth basally; both claws of the hind tarsus (♀♂) rectangularly curved.

Distribution. N. E. Sichuan, CHINA (HAUPT, 1934). SOUTH INDIA, SRI LANKA, TAIWAN.

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RAPID DETERMINATION OF POLLEN FERTILITY OF TWO INSECT POLLINATED PLANT SPECIES BY STAINING WITH THE AID OF PROLINE—ISATIN REACTION

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Abstract

A new rapid staining method has been elaborated for the pollens of *Chrysanthemum leucanthemum* and *Robinia pseudacacia* which can be used to indicate their fertility. With this staining fertility grade of the pollen grains can be seen by different colours. The staining can be performed on living and on fixed pollens as well. Results of the new method is supported by the in vitro observed germination per cent of the pollens and the proline content of their extracts. In marguerite the greatest number of fertile pollens can be collected when the flowers of the outermost circle of the capitulum are open, and fertility of the pollens of the flowers of the inner circles opening day by day centripetally diminishes gradually. The new method can be applied only when the pollen extracts contain at least 1% proline, in the dry matter. Proline content of the pollen extracts of *Helianthus annuus* remains below 0.03%, therefore fertility of the pollens of this species can not determined with the aid of our staining method.

Key words: Chrysanthemum, Helianthus, Insect-pollination, Isatin-reaction, Pollen grains, *Robinia.*

Introduction

Proline content of fertile pollens is extremely high, higher than the amount of the other free amino acids alltogether. Quantity of proline positively correlated with germination per cent and fertility of the pollens (TUPY, 1964; LINSKENS and SCHRAUWEN, 1969; HESLOP-HARRISON, 1971; AHOKAS, 1978; ZHANG et al., 1982).

These results were also proved by RAI and STOSKOPF (1977) on wheat and YAMADA and KONO (1977) on rice and recently by us on corn and rye (PÁLFI et al., 1981; PÁLFI and PÁLFI, 1982; PÁLFI and KÖVES, 1984).

According to HESLOP—HARRISON (1971, 1979), LINSKENS (1974), STANLEY and LINSKENS (1974), MASCARENHAS (1975), ZHANG et al. (1982) and ZHANG and CROES (1983) the important role of proline during germination is its activating effect on respiration and citrat cycle, it is a significant nitrogen source, it regulates water economy, keeps the enzymes in their active form and it is an important component of the proteins of pollen and germ-tube wall in the form of hydroxyproline. The role of proline in the elongation of germ-tube was examined by other authors as well (DASHEK and HARWOOD, 1974; BRITIKOV, 1975; DASHEK and MILLS, 1981).

Pollens of *Lilium longiflorum* were germinated at extremely high and extremly low temperatures in a medium containing ^{14}C-labelled proline (ZHANG and CROES, 1983). The pollens taking up exogeneous proline germinated considerably better than those which were put in the medium without proline. It was concluded that high proline content of the pollens gave them resistance in the case of unfavourable

temperatures and on this way increased the chances of fertilization. Similar results were obtained in the case of drought stress, low temperature treatments and high salt content of the medium by PÁLFI and JUHÁSZ (1969).

Based on the work of LINSKENS (1974), STANLEY and LINSKENS (1974), HESLOP—HARRISON (1971, 1979), DASHEK and MILLS (1981) and ZHANG et al. (1982) we elaborated a rapid staining method using an isatin reagent of new composition, which indicates the proline content of the grains and through this their grade of fertility with conspicuous colours. The results of the new staining procedure were compared with the proline content and in vitro germination per cent of pollens collected at the same time. The outer and inner structure and physiology of dinuclear pollens (dinucleotides) are entirely different from those of the trinucleotide-type pollens which are mostly insect-carried (HOEKSTRA and BRUINSMA, 1979).

Now we pretent our results obtained by isatin staining if trinuclear pollens of three insect-pollinated plant species.

Material and methods

Pollens of the composites marguerite (*Chrysanthemum leucanthemum* L.) and sunflower (*Helianthus annuus* L. cultivar Kisvárdai) and the leguminous robinia (*Robinia pseudacacia* L.) were investigated. In the case of the marguerite first pollens of the flowers of the outermost circle where flowering begins were collected and thereafter dayly that of the flowers of the inner circles as flowering advanced centripetally. In the case of *Robinia* racemes were collected and pollens were separated in the laboratory. In vitro germination of the pollens of three species was also investigated, Composition of the agar-media used is already publiched elsewhere (PÁLFI and KÖVES, 1984).

Proline content of the pollen extracts was determined according to BATES et al. (1973) and the results were controlled with the method of ASPINALL et al. (1973).

A new composition of the isatin-reagent was worked out for pollen staining: 1 ml glacial acetic acid and 1 ml glycerol was added to 100 ml acetone and 0.50 g isatin was dissolved in this mixture (glycerol is not always necessary).

Staining of the pollen grains was microscopically evaluated, therefore the procedure was performed on slides. 2—20 mg pollen was placed on the middle of a slide with the aid of a lancet, two drops of the reagent was added and mixed with the grains till acetone evaporates. This procedure was repeated two times with one drop of reagent. Thereafter the slide was put in *a.* 90 °C exsiccator for ten minutes to develop colours. After cooling down superfluous stain around the pollens was cleaned off with wet cotton wool. A drop of paraffin oil was added to the adhered pollens, they were disperged in it with the aid of a glass rod and the dispersion was spread with a lancet in the middle of the slide. Finally it was covered with a cover glass and slightly pressed.

In the case of living pollens they are fixed by the acetone treatment and the high temperature of colour development. When staining is not performed on the day of collection, pollens should be fixed at 90 °C. The entirely desiccated pollens are stored in hermetically sealed vessels in the dark and their staining can be performed after 12—16 weeks well.

Results and discussion

It can be seen on the microphotos of Figure 1. that pollens of the outermost circle of the capitulum of marguerite are nearly all stained black. These pollens contain the highest quantity of proline and therefore these are for the most part fertile. Evaluating the staining degree of the pollen grains on five fields of sight the per cent of fertility also can be experimentally determined. Advancing to the centre of the capitulum in zones of flowering the proportion of black or dark blue stained pollen grains continually decreases. It means that the fertility grade of pollens lessens in

this direction. Poorly fertile pollen grains stain light blue or light green, sterile pollen grains remain yellow or stain brown (on the black-and white photos different shades of grey). The greatest number of sterile pollen comes from the centre of the capitulum.

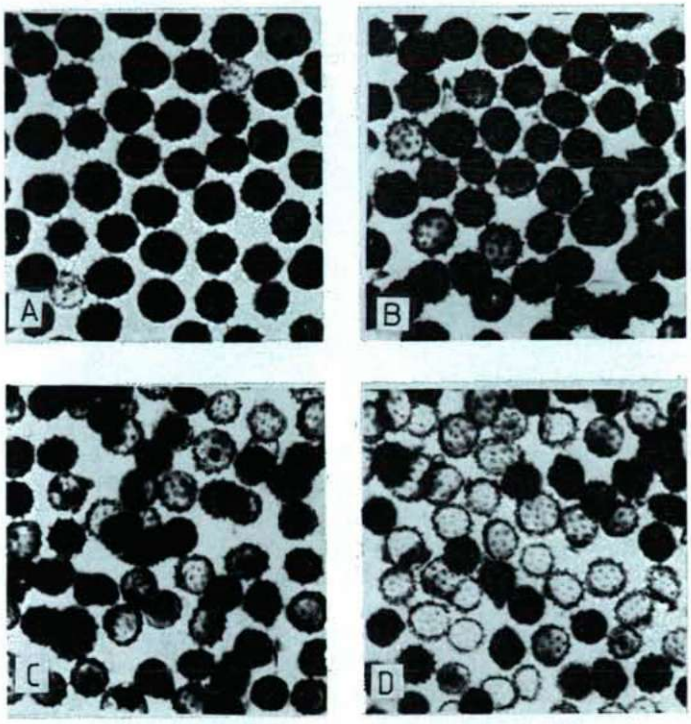

Fig. 1. Approximate determination of fertility of marguerite pollens by rapid staining with the aid of the proline-isatin reaction. Fertile pollens are black, dark grey shades show poor fertility, the light-coloured pollens are sterile. Magnified 300×. The fertility per cent is A)=98%; B)=81%; C)=54%, and D)=42%.

The results of in vitro germination and fertility experiments in the case of the pollens of three species obtained with three different methods are compared on Table 1.

It can be seen on the table that the pollens of *Robinia pseudacacia* germinate rather well in vitro and also their proline content is high. The per cent of grains stained dark (on the Figure they are black) is higher than the per cent of germination.

Pollens of *Helianthus annuus* germinate in higher per cent than those of the former species. The good germination shows that the collection of pollens in living state was successful. Proline content of the extract of sunflower pollens is less than 0.03%. Due to this low proline quantity the cell walls of the grains could not be stained with isatin.

Fertility grade of the *Chrysanthemum leucanthemum* pollens shows identical

Table 1. Comparison of the in vitro germination of pollens, the proline content of the pollen extracts, and the data of staining of the pollen grains with isatin in the case of three insect-pollinated species. Proline content = proline concentration of the pollen extracts in per cent of the dry matter. Staining reaction with isatin is positive (and the pollen is fertile) when the pollen grain becomes dark blue or black. The values in the Table are means of 3 repetition; deviation of the repetitions from the mean is less than ±5%.

Species	Germination per cent in vitro	Proline content %	Positive staining with isatin; %
Robina; *Robinia pseudacacia*	68	1.74	78
Sunflower *Helianthus annuus*	76	0.026	—
Marguerite; flowers of the outermost circle of the capitulum	85	2.15	98
Marguerite; flowers of the second circle of the capitulum	77	1.79	81
Marguerite; flowers of the third circle of the capitulum	47	1.38	54
Marguerite; flowers of the middle of the capitulum	39	1.06	42

tendencies in the three different investigations. The highest values were obtained in pollens collected in the outermost circle of flowers of the capitulum. Proceeding centripetally in the capitulum fertility gradually diminishes and the greatest quantity of sterile pollens was found in the centre. Fertility grades of the pollen grains nearly correspond to the proline levels of the pollen extracts and to the germination per cent in vitro; the staining reaction gives always a higher value than the germination per cent. This can be so interpreted that the staining with isatin indicates the possibility which could be realized if the pollen grains had been living. The investigation of the in vitro germination should be performed on fresh pollens and this can not be perfectly realized in every case.

Our results show that not all insect-pollinated plants have pollens with high free proline content. E.g. *Helianthus annuus* pollens contain very small amount of proline, *Helianthus* is not a proline-type pollen.

Pollens of proline-type species contain more than 1.0% proline in the dry weight. This conclusion was obtained with the pollens of 16 inbred lines and 5 hybrids of corn (PÁLFI et al., 1981; PÁLFI and PÁLFI, 1982), of 5 cultivars of rye (PÁLFI and KÖVES, 1984) and with the pollens of 3 insect-pollinated species in this paper; proline content of the extracts of these pollens was determined and the pollens were investigated with the isatin reagent as well. Other papers also support our results (TUPÝ, 1964; LINSKENS, 1974; STANLEY and LINSKENS, 1974; BRITIKOV, 1975; HESLOP—HARRISON, 1971, 1979; DASHEK and MILLS, 1981; ZHANG et al., 1982; etc.).

It can established that fertility of the pollens of different plant species as well as of different cultivars of these species can be approximately determined on the basis of their proline content with the aid of the rapid isatin staining — if the pollen of species is of the "proline-type". Success of the determination is not influenced by the mode of pollination (by wind or by insects).

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EFFECTS OF ENVIRONMENTAL FACTORS ON ION UPTAKE BY PLANTS*

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Introduction

Environmental factors such as temperature, oxygen supply, pH, etc. considerably affect the ion uptake by plants, hence the mineral nutrition. Detailed investigations of these factors are therefore of importance from both theoretical and practical aspects.

The concept of environmental factors has to a certain extent been widened by the intensive chemicalization of agriculture in recent years, without which modern plant production would hardly be imaginable. The herbicides used in chemical weed control not only destroy weeds, but also influence the metabolism of plants and thereby the yield. Thus besides the classical environmental factors, but because of the possible interactions with them, the individual and general physiological effects of some biologically active substances must be studied. This is necessary for the safe use of the chemically active substances that are indispensable in modern crop production and for the protection of the environment and the biosphere.

The mineral nutrition of plants, or more precisely the uptake of ions, has been especially intensively studied during recent decades, and many valuable data are available for practice too (EPSTEIN, 1972; MENGEL and KIRKBY, 1978). Unfortunately, it can not be said that the mechanism of uptake of nutrients is sufficiently clarified in detail. The research work and the establishment of general regularities are made more difficult by the fact that the differences in uptake of some nutrient elements due to the influence of environmental factors may vary markedly with the plant species (EPSTEIN, 1972; LÜTTGE and PITTMAN, 1976).

Ion uptake by plants can be classified phenomenologically on the basis of the Q_{10} value into two main processes: in one case the Q_{10} value is generally about 1.0—1.2, while in the other it is 2—3 or even higher (SUTCLIFFE, 1962). In the former case the ion uptake is regulated chiefly by physical processes, e.g. diffusion, mass flow, exchange and the passive processes connected with these. In contrast, in the latter case ion uptake occurs primarily in connection with the metabolism, and we therefore speak about an active mechanism.

The effects of environmental factors on these two mechanisms are very different, and depend on the characteristics of the element involved. In general, the effects of temperature, pH and O_2 conditions, but also various biologically active

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compounds, operate, mediated by the metabolically regulated transport processes. If the effects of the environmental factors are not too high the transport processes connected with the metabolism will not be seriously impaired. The reverse of this is true in the case of extreme and sudden changes. There is generally then a stress effect, that may lead directly or indirectly to damage to the membrane and to impairment of the metabolic processes, cell structures, and ion transport connected with the membrane (LEVITT, 1972).

The temperature is an important environmental stress factor from a practical point of view (LYONS et al., 1979). However, the effects of pH and the different biologically active substances, e.g. herbicides, must also be taken account (CARSON, 1974; Audus, 1976). All these factors were considered in the design of our research programme and in the selection of the test plants too.

The importance of the temperature and pH effects has been known for a long tíme but in spite of this both theoretically and practically important questions, especially in connection with thermophilic plants, have not yet been cleared up satisfactorily (LYONS et al., 1979). This is one reason for the fact that endeavours to clarify the consequences of cold damage to thermophilic plants or the consequences of low temperature on the mineral nutrition of plants are still in the initial stage. As concerns the pH effects, the data relating to the different plant species are insufficient and very general. The situation is very similar for some biologically active compounds. In this connection, the herbicides are worthy of special attention; under different environmental conditions, chiefly conditions of temperature and pH, these compounds may influence the mineral nutrition of cereals in very different ways.

Materials and methods

Our investigations were carried out on crops more or less sensitive to environmental factors. One reason for the selection of thermophilic rice as one test plant was the thought that this research might promote the solution of the special and difficult task of Hungarian rice cultivation. It is true that there are a few special traits in the mineral nutrition of rice plants, but some generally known ion uptake processes are to be considered too (FRIED et al., 1965). Another important test plant was wheat a well-known non-thermophilic crop that is especially convenient for comparative investigations. We also investigated other thermophilic plants (e.g. sorghum, cucumber, corn, grapes), to assess the possibility of generalizing conclusions.

Our investigations were made predominantly with the roots of young plants grown in water cultures under controlled conditions. In the investigations of mineral nutrition, the internationally accepted methods were kept in view. Accordingly the low-salt plants were grown in a solution containing 0.5 mM $CaSO_4$. The controlled conditions were insured partly with Conviron, and partly with Vötsch growth chambers.

The short ion transport experiments (influx, efflux), if not mentioned otherwise, relate to a 1 h experiment time. The uptake solution was in general 1 mM. In the case of herbicide treatment, the concentration is given for the active ingredient.

Ion uptake was followed mainly with a tracer technique. Stable and radioactive isotopes were applied in the experiment. Other methods too were used (e.g. atomic absorption spectrophotometry, flame spectrophotometry, etc.).

Measurements on the stable isotope N-15 were made partly in the IAEA Laboratory, and partly in the Austrian Research Centre Laboratory in Seibersdorf. N-15 was determined according to the modified Dumas method developed in the laboratory in Seibersdorf.

The results were generally evaluated through the joint consideration of several data, e.g. ion influx and efflux, and moreover the changes in the quantities of different mineral nutrient and free amino acid contents. As the changes in growth show the reversibility or irreversibility of changes at the cell level, we took this into consideration in the evaluation of stress effects.

The laboratory investigations were occasionally complemented with the results obtained in field experiments at the Research Institute for Irrigation, Szarvas, and the Cereal Research Institute, Szeged, Hungary.

In the experiments relating to the effects of herbicides, the following chemicals were used: Aniten D (2,4-dichlorophenoxyacetic acid+9-hydroxyfluorene-9-carboxylic acid butyl ester); Dikonirt (2,4-dichlorophenoxyacetic acid); Gabonil (4-chloro-2-methylphenoxyacetic acid+3,6-dichloro-2-methoxybenzoic acid); Saturn (S-4-chlorobenzyl-N,N-diethyl-thiolcarbamata); Synpran N (3,4-dichloropropionanilide); Synpran 111 (3,4-dichloropropionanilide+2, 4, 5-trichlorophenoxyacetic acid).

As our investigations with different herbicides soon demonstrated that the physiological effects of auxin-type herbicides to a particularly large extent we initially concentrated our attention on this problem.

Naturally, the still open problems connected with this question are so wide-ranging that a consideration of all their aspects is beyond the limitations of the present discussion. Our investigations were therefore limited to the first steps of mineral nutrition, i.e. to individual relations of the mineral nutrient uptake by roots, and in certain cases only to the study of K^+ uptake.

The key role of K^+ in the maintenance of the structure and physiological functions is well known (INTERNATIONAL POTASH INSTITUTE, 1971). At the same time, the data relating to K^+ uptake, and the changes of its transport due to the effects of environmental factors are rather sparse. As the bulk of K^+ occurs in ionic form in plant cells, for this element the effects of stress factors can be taken into account to a higher degree than for other nutrients. This prompted us to devote special attention to a study of the effects of the environmental factors on K^+ transport (influx, efflux).

During our investigations we dealt with the effects and interactions of some environmental factors, primarily the temperature and pH conditions, and also some biologically active substances (herbicides) influencing the uptake of nutrients by rice and wheat seedlings. Thus, the chief aims of this work extend to the following three closely connected topics:

1. Comparative investigations of the ion uptake and growth of thermophilic and non-thermophilic plants, with special attention to
   — the K^+ uptake occurring in connection with a sudden fall in temperature, and its distribution along the various root segments;
   — the mechanism of ion uptake stimulated by Ca^{++};
   — the structural and growth alterations of cell membranes, caused by a short treatment at low temperature.
2. Study of the effects of the ion uptake and growth, with special attention to
   — the uptakes of K^+, NH_4^+ and NO_3^-;
   — the direct and indirect damaging effects of extreme H^+ concentrations and the role of Ca^{++} in connection with membrane transport stabilization.
3. Study of the interactions between herbicide treatment and some environmental factors, with special attention to
   — the ion uptake by the roots (root zones);
   — the connection between specific herbicide sensitivity and ion uptake;
   — the interactions between pH and the different types of herbicides.

Summary of new scientific results

1. THE EFFECTS OF A SUDDEN FALL IN TEMPERATURE (COLD STRESS) ON THE ION TRANSPORT OF THERMOPHILIC AND NON—THERMOPHILIC PLANTS

1.1. The roots of thermophilic plants show a K^+ uptake (influx) anomaly following a sudden fall in temperature. Consequently, the K^+ influx is considerably higher than would be expected at and near 0 °C.

1.2. As an effect of cold stress, a high-temperature K^+ uptake anomaly can also be demonstrated for thermophilic plants. In this case the K^+ uptake in the physiological temperature range of the plants will be increased by about 50% for a short time. This phenomenon can not be detected with other essential elements or with non-thermophilic plants.

1.3. Similarly to the influx anomaly an efflux anomaly may also be detected: the roots of thermophilic plants lose a considerable quantity of K^+ into the outher medium at low temperature. As concerns the essential elements, the anomaly can be detected only for K^+, and is characteristic only of thermophilic plants (roots).

1.4. At low temperature (10—12 °C) the uptakes of some nutrients may differ considerably: the uptakes of NO_3^- and $H_2PO_4^-$ are much more inhibited than that of NH_4^+, for instance.

2. Anomalous K^+ transport and its characteristics

2.1. The anomalous K^+ uptake appears in a considerably increased absorption process with negative temperature coefficient, the occurrence of which depends critically on the rate of fall of temperature. In the case of gradual coolling, the anomalous K^+ influx is moderated and may eventually cease to come about.

2.2. The concentration of the uptake solution has a marked influence on the absolute value of the influx and on the change with temperature.

2.3. The anomalous K^+ influx is not basically influenced by an uncoupler (e.g. 2,4-DNP), or by a respiration inhibitor. In contrast, however, the pH of the uptake solution and its Ca^{++} content have considerable effects on the process; e.g. under pH 5.5, or in the presence of a certain concentration of Ca^{++}, the anomaly practically ceases.

2.4. There is a close connection between the measure of the influx anomaly and the length of the root (or more exactly its age): the shorter (younger) the root the more expressed the anomaly.

2.5. A correlation can be demonstrated between the low-temperature K^+ influx anomaly and the differing cold sensitivities of some thermophilic species: the more cold sensitive a species, the more intensive the anomalous K^+ influx for a given period of time.

3. The distribution of anomalous K^+ influx along the roots

3.1. The anomalous K^+ influx is restricted to a definite root zone, e.g. exclusively the apical zone in the case of rice, whereas with cucumber — because of the extremely long root calyptra — it is the second 1 cm segment from the apex.

3.2. If the Ca^{++} concentration of the uptake solution reaches a certain value the K^+ influx decreases in all root segments, but especially in the apical meristematic zone.

3.3. At higher temperatures, but still within the physiological temperature range, for both thermophilic and non-thermophilic plants the K^+ influx is the lowest in the apical zone.

4. Studies of ion interaction with special attention to the role of Ca^{++} (Viets effect)

4.1. The degree of Ca-stimulated K^+ uptake (Viets effect) for rice and wheat under low-salt conditions differs, depending on the root segment and the

plant species too. Development of the Viets effect is considerably influenced by the Ca^{++}/K^+ relation and by the ion strength of the uptake solution.

4.2. The Viets effect can be demonstrated only in the range of physiological temperature needed by the plant. For rice this is from 14 to 40 °C, while for wheat it is from 7 to 30 °C.

4.3. The K^+ uptake is considerably inhibited by NH_4^+, but the NH_4^+ uptake is not influenced by K^+. A high (10 mM) concentration of Na^+ stimulates K^+ uptake in the presence of Ca^{++}.

4.4. As concerns the essential elements, the Viets effect was experienced in the uptake of $H_2PO_4^-$ at lower temperatures too, while for NH_4^+ and NO_3^- in the presence of Ca^{++} a smaller inhibitory effect was observed.

5. The distribution of potassium and calcium along the root, and its role in the process of K^+ uptake

5.1. At low temperature (0 °C) in a Ca-deficient uptake solution, the K^{++} content of rice roots definitely decreases. In the presence of Ca^{++}, chiefly the K^+ loss (leakage) of the apical meristematic zone increases further and may reach 30—40%. With the non-thermophilic wheat under similar experimental conditions, only an insignificant K^+ loss appears.

5.2. For rice roots kept in Ca-deficient uptake solution, a K^+ loss can be detected at higher temperature (25 °C), while for wheat this is not experienced; there is even a net K^+ uptake without Ca^{++}.

5.3. In the range of physiological temperature, a Ca-stimulated net K^+ uptake, i.e. a Viets effect, can be demonstrated along the root segments for both thermophilic and non-thermophilic plants. In the apical meristematic region, however, presumably on account of the very high K^+ concentration, this effect does not appear, or to only a very moderate extent.

5.4. The Ca contents of all root segments increases considerably at 0 °C and 25 °C, compared to the untreated control, for both thermophilic and non-thermophilic plants. For thermophilic plants at low temperature, however, there is an essentially higher Ca content in the zone showing a K^+ influx anomaly.

6. The effects of cold stress on the growth of rice and wheat

6.1. Brief cooling of thermophilic plants to 0 °C causes a growth disturbance indicative of damage to the root apical meristematic zone. In roots exposed to the cold stress effect, a considerable structural change and disorganization results after 2—3 days. As a consequence of cold treatment, the root hairs and the underlying 4—5 cell layers of the primary cortex die. At the same time, we could detect no changes in the stele of the roots.

6.2. On the third day after cold treatment the development of side-roots from the one-layer pericycle started at many places. This differed from normal side-root development, however: the supplementation of the decayed tips began in the root-hair zone, and the cell division started simultaneously at more places than under normal conditions.

6.3. The regeneration of cold-treated roots is completed when basiton-type roots are observed externally too, about 14—16 days after cold stress. This phenomenon cannot be observed with the other group (in our case winter wheat) under the same experimental conditions.

7. The effects of pH (H^+ stress) on ion uptake and growth of roots

7.1. With rice at low pH, a K^+ uptake anomaly (influx) can be demonstrated, as a result of which the K^+ influx increases considerably at such concentrations. With wheat under similar experimental conditions, this effect is not noted; increase of the H^+ concentration results in a monotonous decrease of uptake.

7.2. The irregular K^+ influx stimulated by H^+ stress does not result in a net ion uptake; even under such conditions, a K^+ leakage can be noted. The K^+ influx anomaly, made possible by an ion-exchange process, is highly influenced by the ion composition and (predominantly Ca^{++}) the concentration of the uptake solution.

7.3. In the uptakes of NH_4^+, NO_3^- and $H_2PO_4^-$ ions, a pH-stimulated anomaly can not be detected for either rice or wheat. The uptakes of these ions proceed as expected.

7.4. The growth of rice and wheat between pH values of 5 and 10 is undisturbed. Unexpectedly, more extreme (acidic or alkaline) pH conditions are tolerated better by rice than by wheat. As with cold stress, sudden changes play an important role in this case too.

8. The effect of herbicides on the nutrient uptake by roots

8.1. Low (10^{-6}—10^{-8} M) herbicide concentrations are generally stimulatory, while higher ones (1.0—0.1 mM) have inhibitory effects. For both inhibition and stimulation, however, important differences are noted for certain nutrients. Our investigations showed the K^+ and NO_3^- uptakes to be much more sensitive to herbicide treatment than those of NH_4^+ or $H_2PO_4^-$.

8.2. At higher herbicide concentrations (1.0—0.1 mM), the cell membrane can be directly damaged, which causes considerable ion and free amino acid leakage.

8.3. A pH decrease strongly increases the uptake of auxin-type herbicides, and hence the disturbing effects of their ion uptake and growth inhibition. For non-auxin-type herbicides, the change of pH does not influence the phytotoxic effects of the compounds.

8.4. The temperature coefficient (Q_{10} about 1.7) of 2,4-D uptake and the accumulation of 2,4-D experienced in the roots suggest that the initiated influx of auxin-type compounds may be a process requiring energy.

8.5. Even at a concentration of 0.01 mM, auxin-type herbicides cause a considerable growth disturbance, primarily in the roots. The roots are more sensitive than the shoots to auxin herbicides. The reduction in the root growth was not in accordance with the dry matter production or mineral content: the higher the growth disturbance, the higher the mineral content in the root.

9. COMPARATIVE INVESTIGATIONS OF HERBICIDE SENSITIVITY

9.1. Following different herbicide treatments, marked differences can be observed in the ion uptakes of wheat and rice roots and root segments. With increase of temperature, the inhibitory effects of herbicides on the ion transport and growth of plants, especially thermophilic rice, increase.

9.2. Some crops show different sensitivities to different herbicides as concerns ion uptake, growth and dry matter production. The GK 3 wheat species, for instance, is less sensitive to 2,4-D than to MCPA treatment, while in the case of the Rannaja 12 species the reverse is true. The Dunghan Shali rice species is much more sensitive than Szarvasi 70 to 2,4-D.

9.3. At higher temperatures, 0.1—0.01 mM herbicide generally decreases the ion uptake of all root zones, while at low temperatures the uptake system of the older (more differentiated) zones is damaged.

9.4. 2,4-D uptake by rice roots and its transport to the shoots is faster than in wheat. This may partly explain the different herbicide sensitivities experienced for some crops. At low temperatures (for wheat, 5 °C, for example) the uptake (transport) and unfavourable physiological effects of herbicides practically cease.

New basic results and their practical importance

1. Depending on the K^+ influx response to a sudden fall of temperature (cold stress), plants can be divided into two main groups. Those thermophilic at or near 0 °C show an anomalous K^+ influx, while this is not characteristic for the non-thermophilic group. Our investigations so far suggest that the K^+ influx anomaly resulting from passive ion-exchange is one of the determining features of thermophilic plants.
2. There is a definite relation between the cold resistance of thermophilic seedlings and the extent of the K^+ influx anomaly. Measurements of changes in K^+ influx due to exposure to low temperature can therefore be used to estimate varietal differences in cold-resistance: a test procedure is proposed for the screening of newly bred or newly introduced thermophilic varieties for temperature-sensitivity.
3. Under acidic stress conditions, roots of thermophilic plants undergo changes in plasma membrane composition and structural organization, resulting in a K^+ influx anomaly and leakage. The K^+ influx and K^+ content data indicate that, under these conditions, cytoplasmic K^+ readily exchanges with labelled K^+(^{86}Rb) in the presence of zero or low Ca^{++} concentration.
4. Ca^{++} not only eliminates the K^+ uptake anomaly but reverses the anomalous K^+ influx. From the above facts it can be concluded that the K^+ uptake anomaly is a phenomenon connected primarily with the plasmalemma of roots, i.e. there must be an essential difference between the thermophilic and non-thermophilic plant root cells as concerns the composition and/or structure of the plasmalemma.
5. The transport characteristics and ion transport relations of the plant roots are heterogeneous. The marked (3—4-fold) K^+ concentration gradients between the root segments (apical zone and differentiated zones) show that chiefly metabolic processes take part in their maintenance.

6. Under stress effects a considerable leakage of different nutrients, and primarily K^+, must be taken into account. Under such conditions, therefore, or later, mainly those organs (root zones) are damaged which use a relatively high K^+ concentration for the normal physiological functions. It is not surprising that for thermophilic plants, e.g. in the effect of cold stress, (irreversible) changes occur in the apical meristematic zone that lead to the disorganization (death) of the root apex, the cessation of elongation growth and irregular side-root development. All this repeatedly draws attention to the especially important physiological function of K^+.
7. To arrive at a correct understanding of the mechanism of ion uptake by roots, it is absolutely necessary to take into consideration the different behaviours of some root zones. The varied behaviour of the root zones at low temperature, and especially that of the apical meristem, deserves special attention from both a methodical and a general physiological point of view.
8. The effects of auxin-type herbicides on ion uptake and transport (and hence growth) depend critically on the pH. Their proper application therefore demands a consideration of the chemical properties of the soil.
9. As concerns the uptakes of different nutrients, important differences can be observed between plant species on the action of herbicides. This condition must be taken into account in solving actual tasks connected with agrochemical processes (fertilizing, chemical weed control, etc.). This is especially so for thermophilic plants that are exceptionally sensitive to different environmental stress effects (sudden changes).

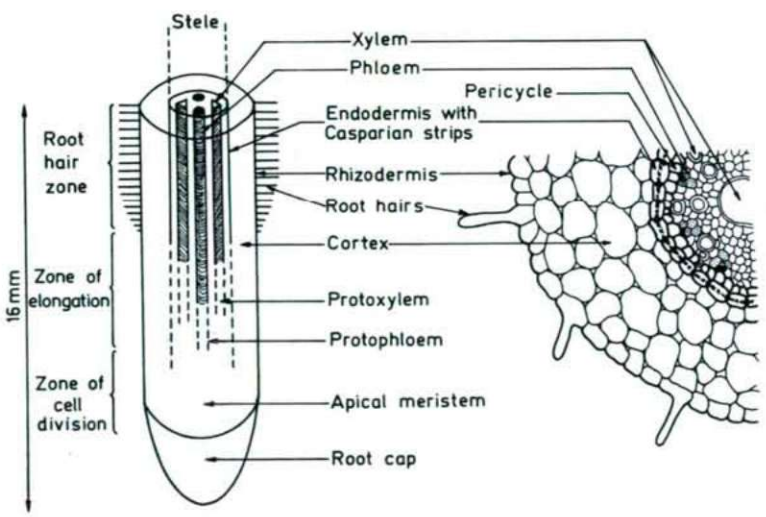

Fig. 1. Root anatomy. A) Diagram of a root tip showing the spatial relations of different tissues and order of maturation. B) Cross-section of a root of a monocotyledon. (Modified after ESAU 1969).

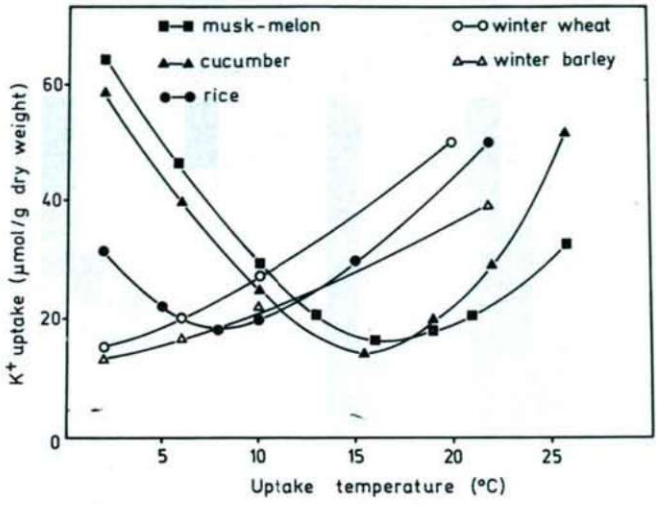

Fig. 2. Temperature-dependence of initial K^+(^{86}Rb) uptake by excised roots of various plants after sudden cooling of the uptake temperature. Absorption solution: 0.5 mM KCl; uptake time: 50 min. (Connected sections: 1.1, 1.4, 2.1, 2.5; and publications: 1, 3, 5, 13, 32, 35).

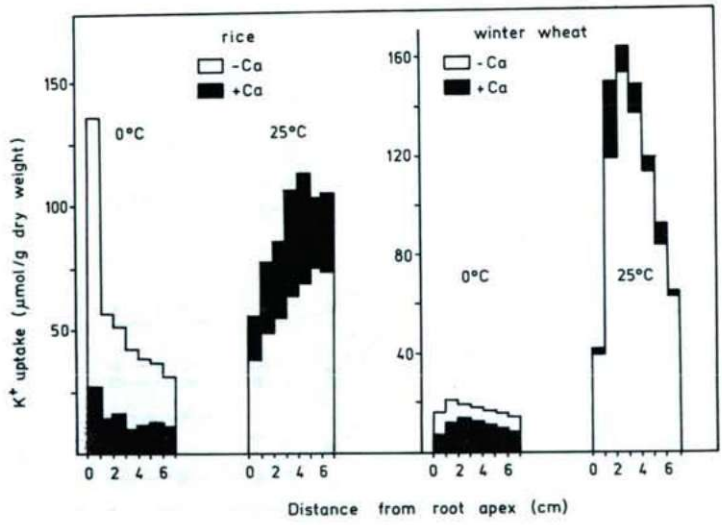

Fig. 3. Effects of Ca^{2+} and temperature upon K^+(^{86}Rb) uptake distribution patterns along primary roots of rice and winter wheat. Absorption solution: 1 mM KCl with or without 1 mM $CaCl_2$; uptake time: 60 min. (Connected sections: 3.1, 3.2, 3.3, 4.1; and publications: 17,18, 25, 26, 32).

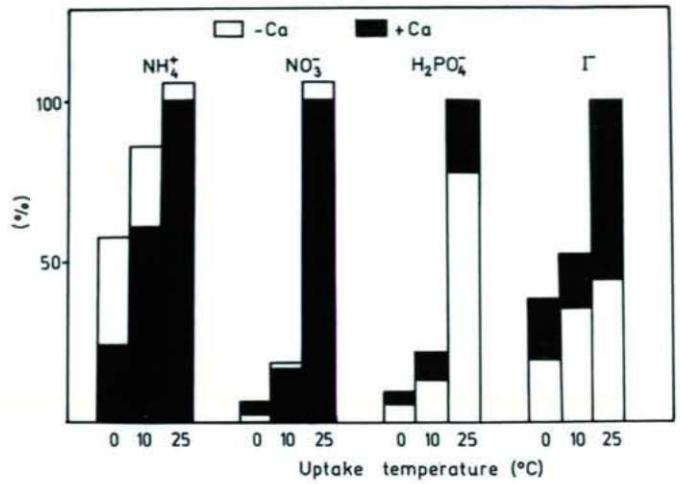

Fig. 4. Temperature-dependence of initial uptake of different ions by excised rice roots after sudden cooling to the uptake temperature. The labelled absorption solution contained 0.5 mM of NH_4Cl, $NaNO_3$, NaJ each and 0.1 mM KH_2PO_4, respectively. Uptake time: 60 min. (Connected sections: 1.4, 4.4; and publications: 9, 12, 32).

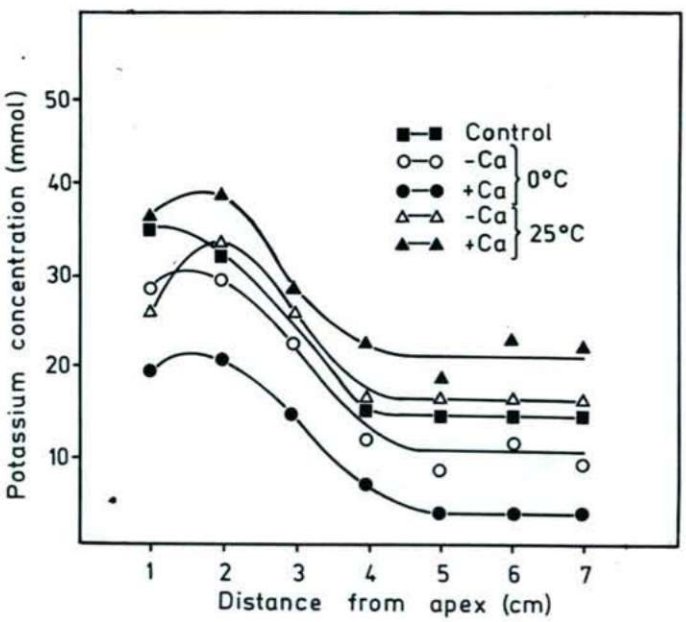

Fig. 5. Concentration distribution of K^+ along rice root (ORYZA SATIVA *L.* cv. *Dunghan Shali*) in the presence and absence of Ca^{2+} at 0 and 25 °C. Otherwise as in Fig. 3. (Connected sections: 5.1, 5.2, 6.1, 6.2, 6.3; and publications: 29, 30, 34, 35, 36, 37).

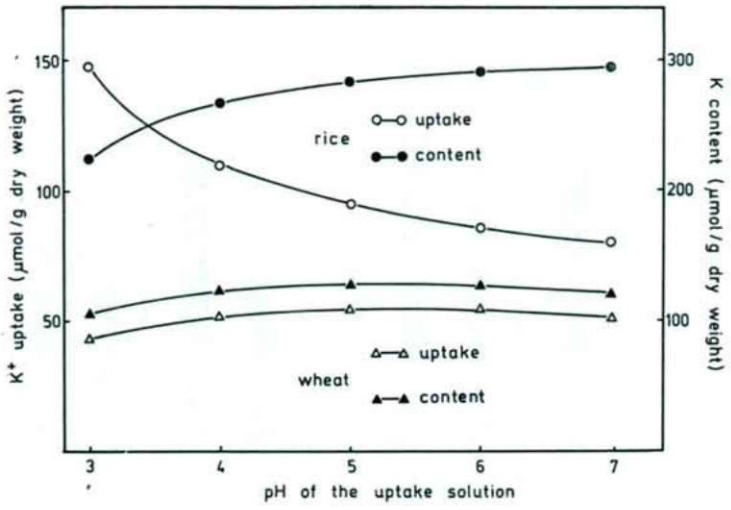

Fig. 6. Effect of pH on K^+(^{86}Rb) uptake and K^+ content of excised rice and winter wheat roots. The uptake solution contained 1 mM KCl+0.5 mM $CaCl_2$; otherwise as in Fig. 3. (connected sections: 7.1, 7.2; and publications: 34, 35, 36, 37).

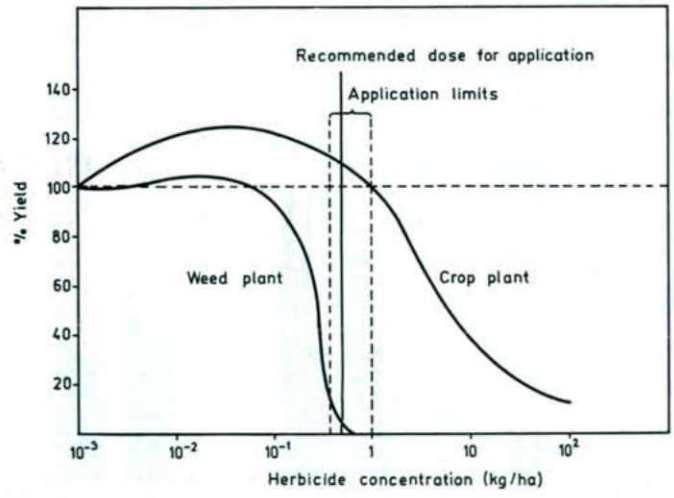

Fig. 7. The influence of different doses of a herbicide on the yield of crop plant and weeds. After LINSER (1976). (Connected sections: 8.1, 8.2, 8.5; and publications: 15, 19, 22, 24, 27, 28, 29, 31, 36).

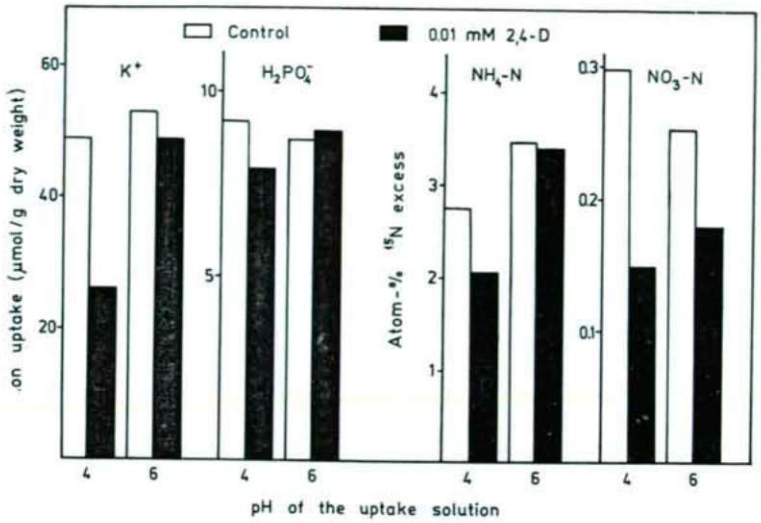

Fig. 8. The effect of 2,4-D on the uptake of K^+, $H_2PO_4^-$, NH_4^+ and NO_3^- ions of rice roots at different pH values. The uptake solution contained 1 mM $K(^{86}Rb)Cl + 0.5$ mM $CaCl_2$; $^{15}NH_4Cl + 0.1$ mM $CaSO_4$; $Na^{15}NO_3 + 0.1$ mM $CaSO_4$ each and 0.1 mM $KH_2{}^{32}PO_4 + 0.5$ mM $CaCl_2$, respectively. Otherwise as in Fig. 3. (Connected sections: 8.1, 8.3, 8.4; and publications: 27, 30, 36).

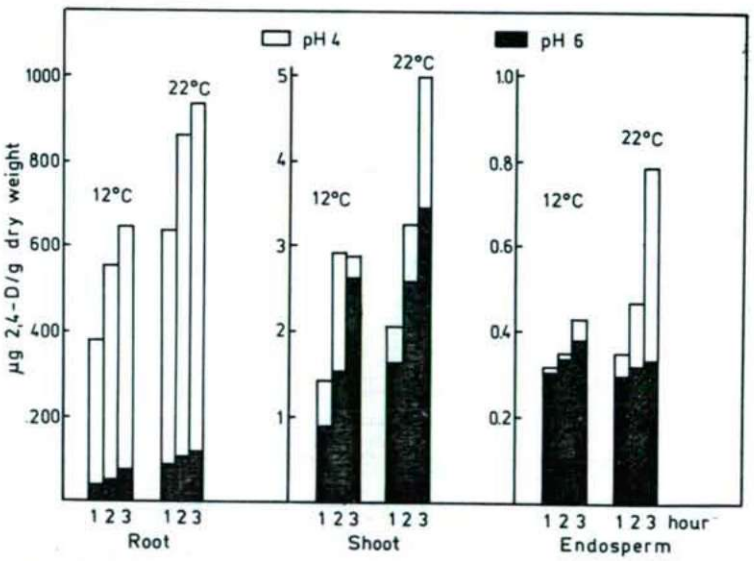

Fig. 9. The effects of pH on the uptake of 2,4-D and its transport within rice seedlings. The uptake solution contained 0.01 mM ^{14}C-2,4-D + 0.5 mM $CaCl_2$. The uptake time was 1, 2 and 3 h. (Connected sections: 8.4, 9.1, 9.3; and publications: 29, 30, 36).

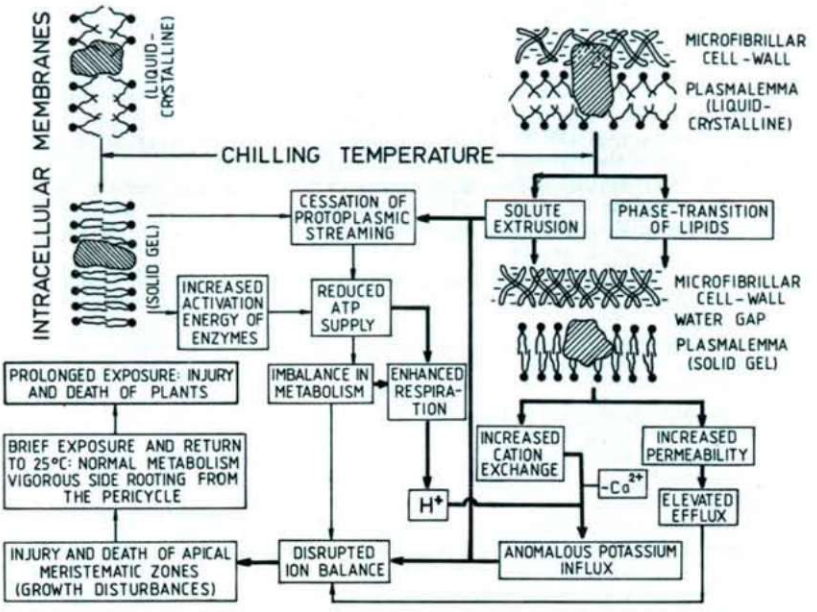

Fig. 10. Suggested schematic pathway of membrane-linked events involved in chilling injury of the apical meristematic zones of thermophilic plant roots. The model is an extension of that proposed originally by LYONS (1973).

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ADAPTATION OF THE MEMBRANEOUS SYSTEM OF BEAN CHLOROPLASTS TO IDENTICAL AND ALTERNATING LIGHT-DARK PERIODS

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Abstract

The growth of Cherokee bean leaves, the degree of dry matter accumulation and the transformation of the membraneous system of palisade chloroplasts were studied:
1. in identical 16—8 hrs, 30—15 min and 15—7.5 min light-dark periods (LDPs) for 5 weeks,
2. as well as in plants grown in LDP changed after the first 3 weeks.

It could be determined that the short-rhythm treatments stimulated the growth of the plants, the development of the leaf and flower initiatives, and increased the area of the leaf.

In the short (30—15 and 15—7.5 min) LDPs identical for 5 weeks the accumulation of dry matter increased for 3 weeks, then decreased compared to the 16—8 hrs LDP.

The plants adapted to various LDPs were further grown in new LDP after 3 weeks (for 2 weeks). At the age of five weeks, the mass of dry matter significantly increased in the case of plants placed from short LDP to long LDP, and decreased in the case of those transferred from long LDP to short LDP.

Positive correlation with dry matter production was found to be the tightest regarding the total membrane/unit cut surface and the partition lengths, as well as the enhancement of thylakoid aggregation. The size of the plasts was in negative correlation with the accumulation of the dry matter.

Key words: light-dark period, dry mass, chloroplast, granum, stacked and unstacked membranes.

Introduction

The development of plants depending on the length of light-dark periods (LDPs) has been known since the beginning of the century. Nevertheless, there are still authors — e.g. SAGER and GIGER (1980) — according to whom the efficiency of photosynthesis cannot be greater in intermittent light, than in continuous light. We have already reported in several papers that in phytotron, besides identical daily illumination and light intensity, the plants may produce considerably more, or less by applying LDPs of various lengths than in long-day illumination of 16 hrs. According to our studies so far, the 30—15 min light-dark cycle is of transitional character, increasing and decreasing, resp., the light utilization of the plants depending on species, type and genotype. On the contrary, the 15—7.5 min LDP is uniformly unfavourable in respect to plant growth (HORVÁTH and MIHALIK, 1978; MARÓTI and PATAKY, 1982; MARÓTI and MIHALIK, 1983; MARÓTI and TAKÁCS, 1983).

In our experiments the daily illumination (16 hrs) and light intensity (32 W/m^2) were identical, but the light-dark periods (LDP) of 2—1, being similar to the long-day illumination, alternated every 30—15 and 15—7.5 min. The 16—8 hrs LDP was regarded as control. These short cycles had significant effect on the development of the plants as well as on the structure of the chloroplast. One of their main effects

was that the thylakoid number per granum decreased, but normal grana, stroma lamellae developed (MARÓTI and TAKÁCS, 1983; MARÓTI and PATAKY, 1983), thus basically differed from the light-dark periods of 1/40—1/90 in which cases only primary thylakoids were formed (ARGYROUDI et al., 1976; ARNOND et al., 1976; AKOYUNOGLOU et al., 1978).

The short LDP is similar to the short and long alternations of light and dark in that it firstly changes the light-harvesting complexes and their pigments, respectively (MARÓTI, 1982).

DAVIS et al. (1976) and HORTON et al. (1978, 1980) reported on similar experiments. These authors determined that the transfer from intermittent to continuous light increases the photosynthetic units, resulting firstly in the appearance of the LHC a/b proteins, 12 hours later the differentiation and aggregation of the thylakoid membranes are complete, the concentration of chlorophyll increases and the chlorophyll a/b decreases, resp. The aim of the present paper was to study the effect of the changed LDPs on the development of the plants. Answer was sought to the question, to what extent and how fast are the plants already accommodated to LDP of certain lengths capable of conversion to the new rhythm, and how determinant is the light-dependent prelife?

A main question is whether there is any relationship between the biometry of the membraneous system of chloroplasts and the utilization of light energy. The utilization of energy was followed on the basis of measuring the dry matter production. First the degree of thylakoid aggregation, as well as the relationships between the ratio of the adnated and single membranes and dry matter production were evaluated.

Materials and methods

In our experiments bean plants (*Phaseolus vulgaris* L. cv. *Cherokee*) were grown in phytotron (HORVÁTH, 1972) in the mixture of sand-perlit 1:1 which was humidified at the time of sowing with modified Hoagland nutrient solution in an amount corresponding to 80% of the water capacity (REYSS and BOURDU, 1971). The aliment supply was ensured with 20 ml nutrient solution twice a week and water supply with destilled water daily. F_{29} light tubes were used for illumination. The light intensity was 32 W/m²; the daily total illumination 16 hrs; the temperature 20 °C ± 2; and the humidity of the air 50—70%.

1. IDENTICAL SHORT-RHYTHM TREATMENT

One part of the plants were grown in identical LDP from the time of sowing till processing (5 weeks) in which case the plants received three kinds of treatment. The control plants were grown in 16 hrs light and 8 hrs dark period. Two types of short rhytms were applied, in one 30 min light and 15 min dark alternated repeatedly for 5 weeks. In the other short cycle 15 min light and 7.5 min dark alternated.

2. VARYING LIGHT-DARK TREATMENT

In another part of our experiments the plants were transferred to new LDP at the age of three weeks. This was the treatment of varying rhythm. The development of the leaves was followed with attention, the length and width of the primordial and tripartite leaves were measured every second day. The plants were processed at the age of 3 and 5 weeks. The dry mass was measured after drying at 70 °C.

For electronmicroscopic studies samples were taken from the central part of the lateral leaflet of the first tripartite leaf at the age of 5 weeks. The leaf pieces with diameters of 0.5—1 mm were placed in Karnovsky fixative (HALL, 1978) then contrasted with 2% OsO_4 and 2% $KMnO_4$, respectively. The leaves were embedded in Durcupan ACM resin and the sections prepared with Reichert ultramicrotome were stained with Pb-citrate. Pictures were made of the chloroplasts of the palisade cells with TESLA BS 500 electronmicroscope. From the pictures of known magnification the planar size of the plasts, the size and number per unit area of the grana, the htylakoid number per granum

(degree of thylakoid aggregation) and the length and ratio of the stacked (partition) and single membrane (stroma lamella, end granal membrane/were evaluated. The length of the membranes and the value of the granal surface ratio were estimated from the whole cut surface of the chloroplasts, also including the starch area. 20—30 plasts were evaluated per treatment. The greatest length and width of the plasts were measured on semithin sections.

Results

1. Effect of identical and varying short LDPs on the dry matter accumulation and leaf growth

At the age of 3 weeks the dry mass of the bean plants grown in 30—15 min and 15—7.5 min LDPs exceeded the dry mass of the plants grown in 16—8 hrs LDP by cc. 10%. Only the initiative of the youngest tripartite leaf appeared during the long

Table 1. The effect of the light-dark periods of different lenght on the dry-matter quantity of 3-week old bean plants.

Light treatment	Dry-matter mg/plant					
	root	stem + petiolus	primordial leaves	l. tripartite leaves	other leaves	total
16—8 hrs LDP	166.7	116.1	165.1	14.4	3.1	466.0
30—15 min. LDC	179.2	129.2	152.3	37.7	5.9	504.3
15—7.5 min LDC	162.5	133.3	126.9	58.0	11.4	492.1

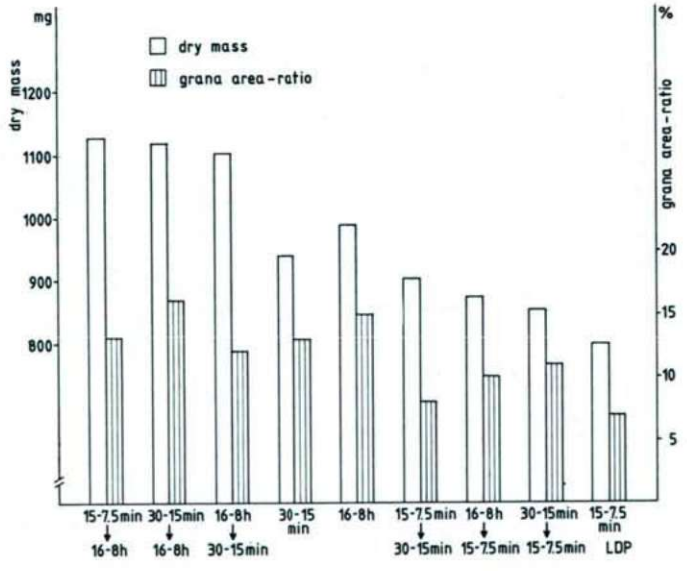

Fig. 1. Changes of total dry mass (mg/plant) and grana area-ratio in 5 weeks old bean plants in identical and alternating LDPs.

day illumination, in the short rhythm these leaves were moderately developed. It was also manifest from the dry mass measurements regarding each plant that the amount of dry mass of the older, developed primordial leaves was less in the short rhythm and that of the young leaf was 2—3 times more compared to the control (Table 1).

The effect emphasizes that there were no buds on the bean plants grown in 16 hrs illumination at the age of 4 weeks, in the 30—15 min cycle violet-coloured buds were found, and in the 15—7.5 min rhythm the beans already flowered.

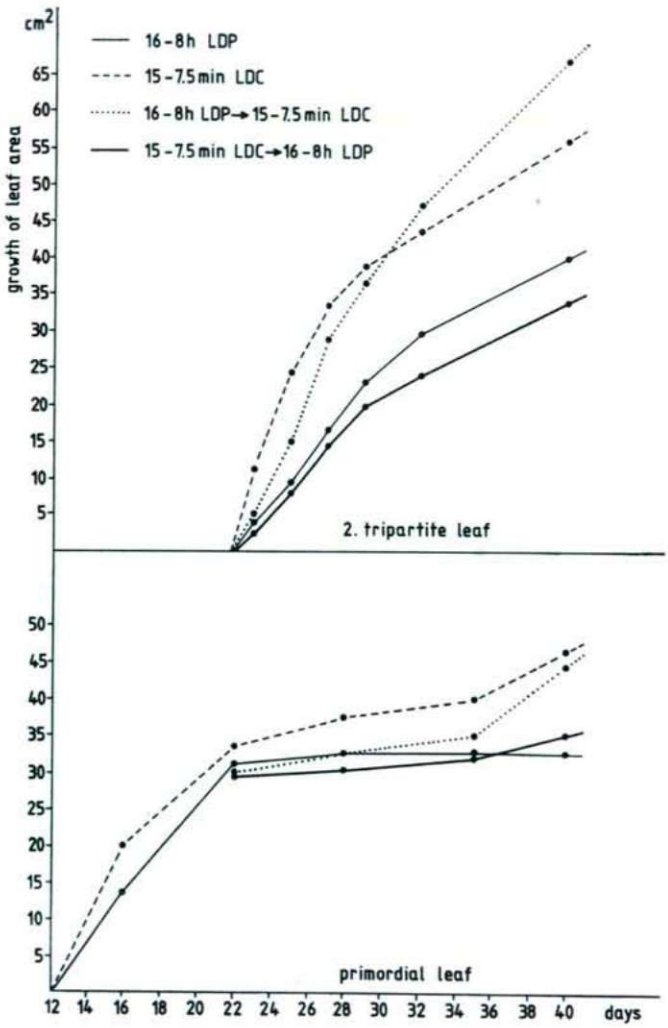

Fig. 2. Effect of identical and alternating LDPs on the area-growth of the primordial and 2. tripartite leaf.

The total dry matter of the plants grown for 5 weeks in identical 30—15 min LDP decreased slightly compared to the control and was about 20% less in the 15—7.5 min LDP (Fig.1).

From the plants grown in varying cycles the dry mass of those increased which grew in shorter (30—15 min and 15—7.5 min) LDPs for the first 21 days and were then transferred to the 16 hrs continuous light for 2 weeks.

Similar increase in dry matter compared to the continuous illumination could also observed when the plants were placed from the 16—8 hrs cycle to the 30—15 min rhythm.

A decrease could be observed in the accumulation of dry matter when the plants were placed from longer LDP to the 15—7.5 min LDP, and also in the case of changing the two short rhythms. The production of the beans grown for 5 weeks in 15—7.5 min cycle was the lowest of all variaton (Fig. 1).

It could be observed from the measurements of leaf growth (Fig. 2) that during the long-day illumination growth rate of the leaves was moderate, growing less quickly. After transfer the new rhythm had less effect on the growth of the older leaves. New LDP only merely affected the development of the primordial leaves, even after transfer they grew at the rate characteristic to the original rhythm. The young tripartite leaf rapidly accommodated to the growth rate characteristic to the new LDP.

Transfer from longer to shorter cycle resulted fast development regarding the young leaves, e.g. the growth of the leaf area was 5 times greater in the case of transfer from 16—8 hrs to 15—7.5 min cycle, than in the case of plants grown for 5 weeks in 16 hrs light.

2. The effect of identical and various LDPs on the structure of the chloroplast

There was an increase in the size of the chloroplasts of the palisade parenchyma on the effect of the short cycles, and even a change was detectable in the shape of the plasts; they became elongated, flattened (Plate I). In control leaves the length of the plasts was 5.5 μ and their width 3.5 μ. On the effect of short rhythm treatment their length increased to 7.5—8 μg and their width to 4 μ. The cut surface of the chloroplasts of plants grown in long-day illumination was occupied by starch in 15—20%, the membraneous system was found in the peripheral parts (Plate I).

The characteristic effect of the short LDPs on the structure of the plasts was also expressed by the lack of accumulation of assimilative starch. The amount of primary starch was also similarly low (1—2%) in the case of transferred plants where the production showed a decrease compared to the control (Plate IV). In the case of plants placed from short rhythm to 16 hrs continuous light, the considerable amount of dry mass was accompanied by high amount of assimilative starch (Plate III). The number and size of grana, as well as the changes in granal surface-ratio were also studied. The amount of grana found on the entire cutsurface was the largest in the case of the shortest cycle. It was also of similar high value in the plants transferred from 15—7.5 min LDP to 16 hrs illumination. In the leaves grown at continuous light the total grana amount was averagely 15%. The 30—15 min LDP treatment also was close to this value. The 15—7.5 min rhythm decreased the quota of grana by more than 50% (Fig. 1).

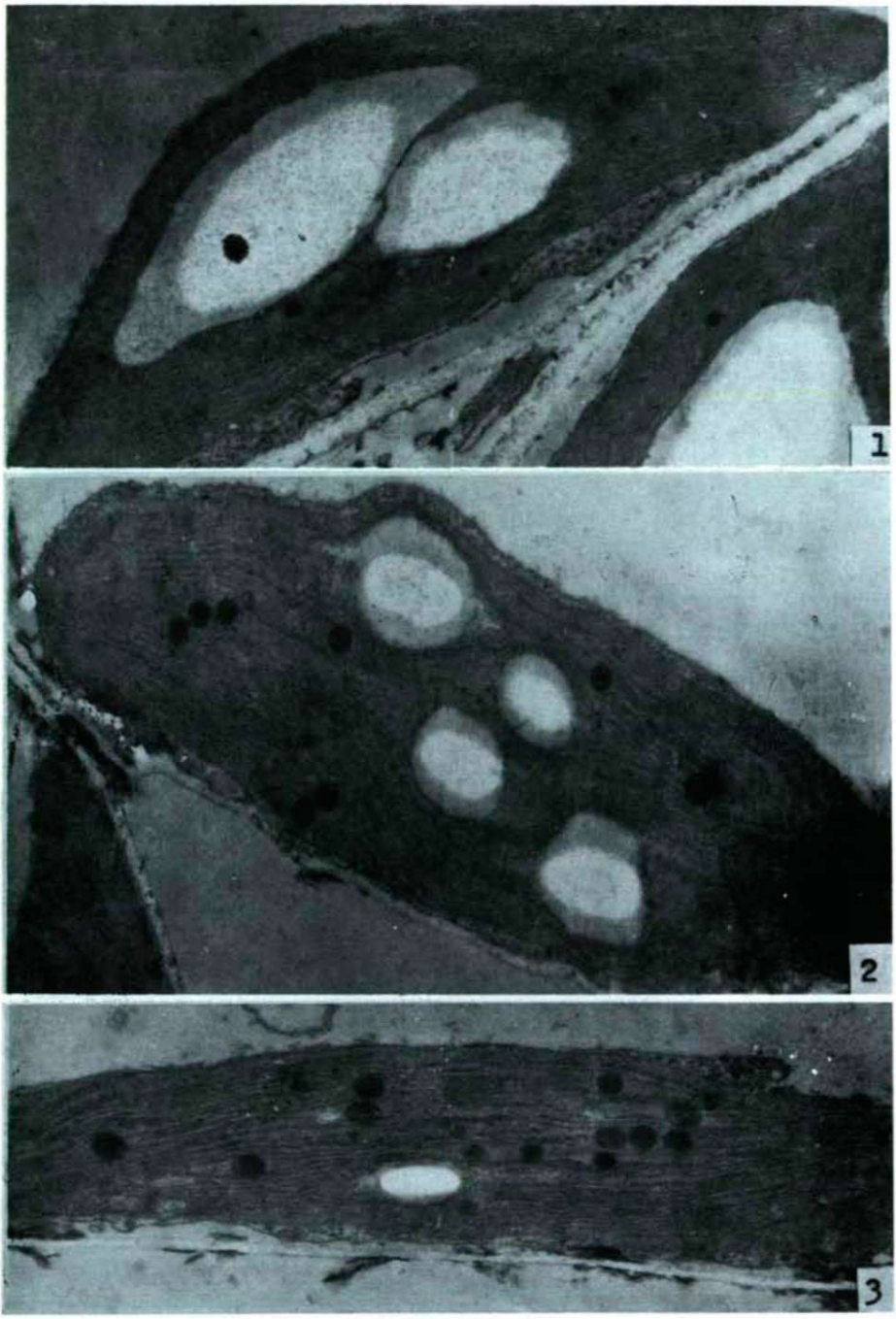

Plate I.

1. light-dark cycle 16—8 hrs (25 000×)
2. light-dark cycle 30—15 min (25 000×)
3. light-dark cycle 15—7.5 min (25 000×)

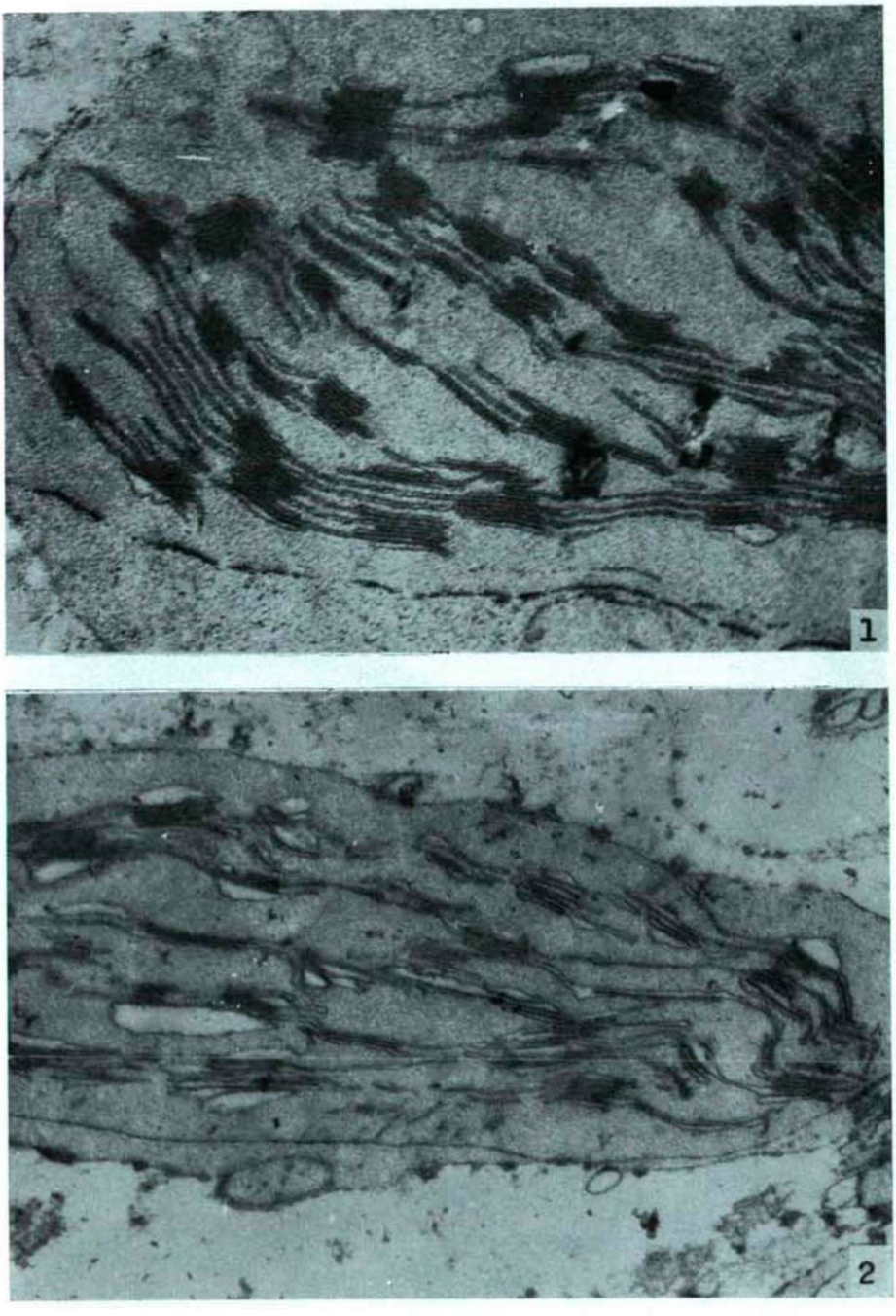

Plate II.

1. light-dark cycle 15—7.5 min (35 000×)
2. light-dark cycle 15—7.5 min → 30—15 min (35 000×)

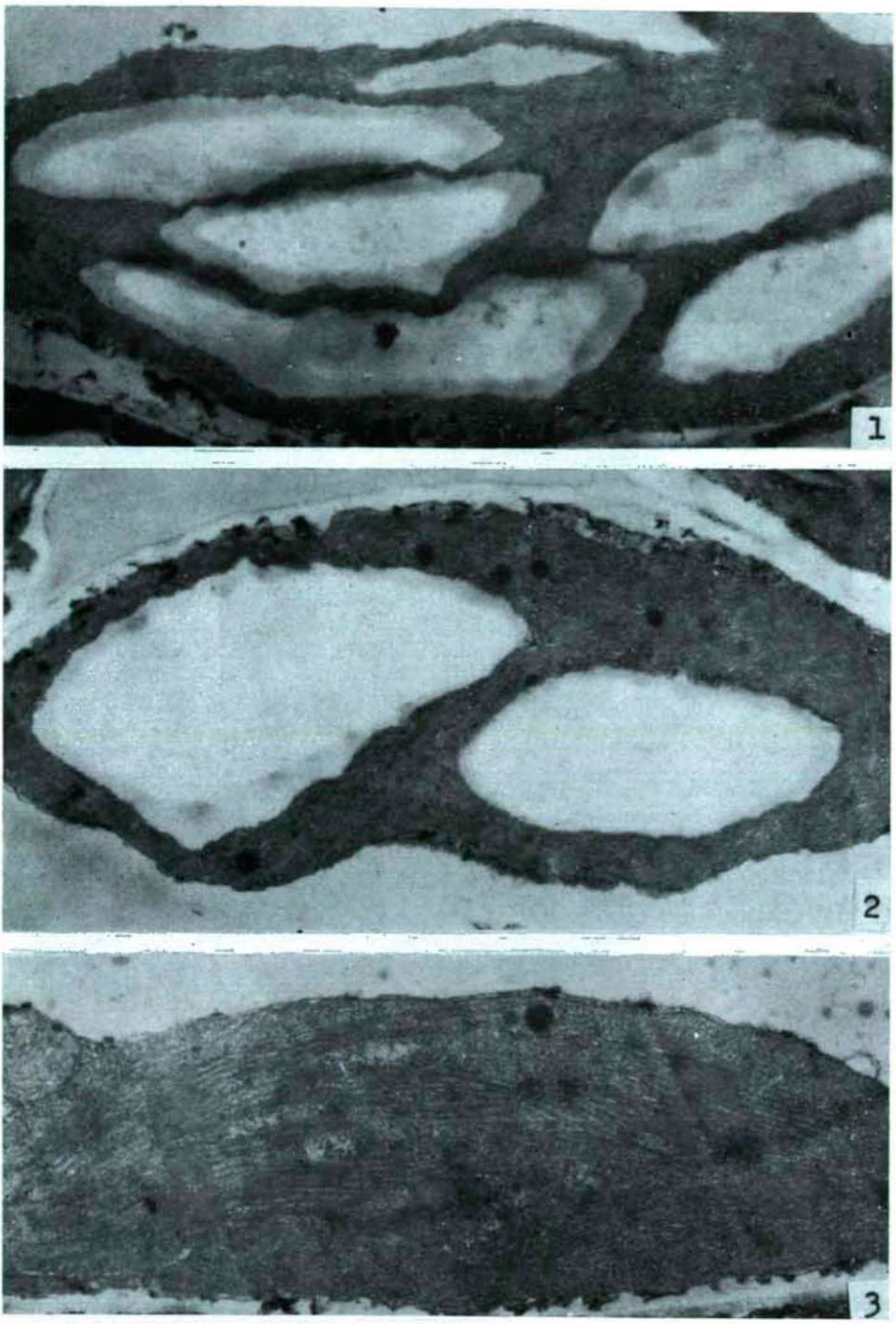

Plate III.

1. light-dark cycle 15—7.5 min→16—8 hrs (25 000×)
2. light-dark cycle 30—15 min→16—8 hrs (25 000×)
3. light-dark cycle 16—8 hrs→30—15 min (25 000×)

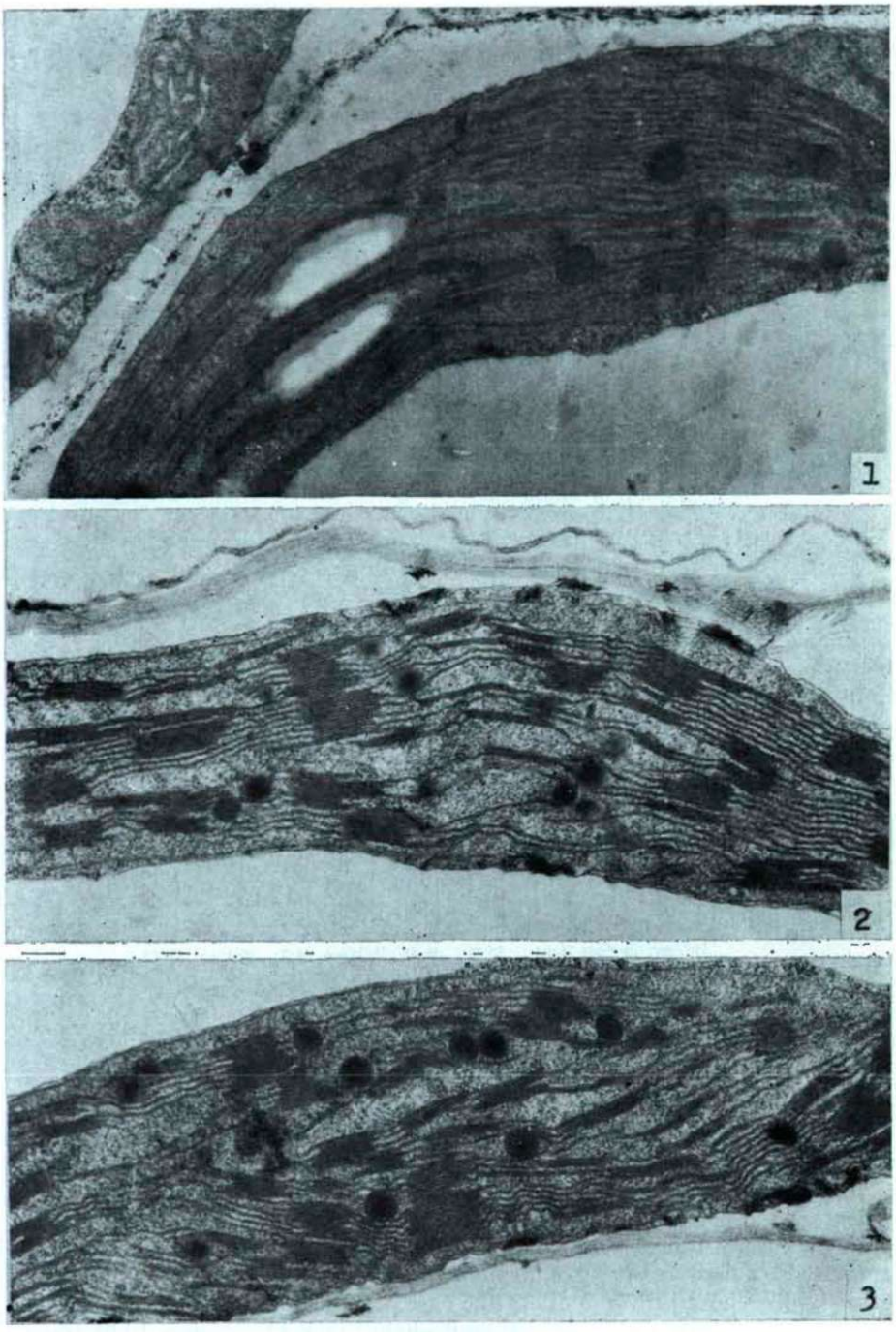

Plate IV.

1. light-dark cycle 16—8 hrs→15—7.5 min (25 000×)
2. light-dark cycle 30—15 min→15—7.5 min (25 000×)
3. light-dark cycle 15—7.5 min→30—15 min (25 000×)

On the basis of thylakoid aggregation, grana were separated into three groups: grana composed of 2—9 (few); 10—21 (average); 22—35 (many) thylakoids (Fig. 3).

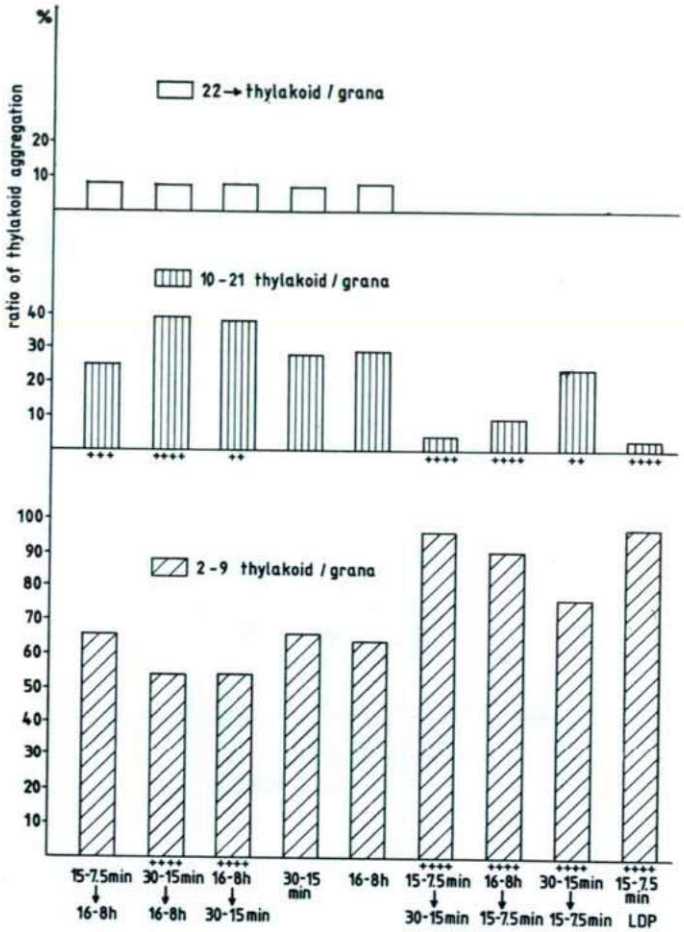

Fig. 3. Effect of identical and alternating LDPs on the degree of thylakoid aggregation. Significance: P=10% +; P=5% ++; P=1% +++; P=0,1% ++++.

In the plasts of leaves grown in long-day illumination and 30—15 min LDP the grana standing of 10—21 and 22—35 thylakoids occurred in about 40%.

In the 15—7.5 min LDP grana stacked by 2—9 thylakoids dominated, their frequency was 98%. Grana made up of high columns did not develop.

In the case of transferred plants where the production of dry matter increased, there was also a high frequency of medium and large-sized columnar grana developed by the tightly stacked thylakoids. In the case of bean plants transferred from one short cycle to another, and from continuous light to the 15—7.5 min LDP, respecti-

vely, the degree of thylakoid aggregation became slighter parallel with the decrease in production, and grana composed of 20—30 thylakoids were not observable either.

The partition of the multithylakoidal grana was short, their height per width ratio was high. The partition surface of the grana discs increased with the decrease in thylakoid aggregation. The conformation of the thylakoids showed considerable change on the effect of the 15—7.5 min short cycle. In one part of the plasts the grana. intrathylakoidal spaces became swollen, expanded. The loculi of the end discs dilated into wide sacks at many places. Similar dilatation could also be observed in respect to the stroma lamellae. Many vesicules were found at the edge of the stroma lamellae. These dilating processes were not characteristic to every plast membrane, but these manifestations proceeded in about half of the studied chloroplasts, in smaller-higher degree (Plate II).

Table 2. Effect of identical and alternating LDPs on the organization of the thylakoid membranes of the palisade chloroplasts in the 1. tripartite leaf.
Significance: P=10%+; P=5%++; P=1%+++; P=0,1%++++

Light treatment	Number of grana/ chloroplast section area	Total lamellar material μ/μ^2	Partition lenght μ/μ^2	Stroma lamellae μ/μ^2	End granal membrane μ/μ^2	Proportion of		
						partition	stroma lamellae	end granal membrane
						to total lamellar material		
16—8 hrs LDP	39	30	18	8.6	3	61	28	11
30—15 min ↓ 16—8 hrs	37	27	15	8.1	3.3	57	30	12
15—7.5 min ↓ 16—8 hrs	56	27	16	7.2	3.4	60	27	13
16—8 hrs ↓ 30—15 min	32	21++	13++	6.7+	2.1+	59	31	10
30—15 min LDC	38	21++	12+++	6.3+	2.5+	57	30	12
15—7.5 min ↓ 30—15 min	34	16+++++	7.5+++++	5++	3.3	47	33	20
30—15 min ↓ 15—7.5 min	31	17+++	9++++	5++	2+	55	22	13
16—8 hrs ↓ 15—7.5 min	34	19+++	9++++	6.7+	3.6	47	34	19
15—7.5 min LDC	54	11+++	5++++	3+++	3.4	44	26	30

The ratio of the stacked and single membranes was also studied and the membrane length per unit area was evaluated (Table 2). Answer was sought how the membrane organization of the chloroplasts changed if the plants were grown further in another LDP.

The 9 variants could be divided into 2 groups, from the viewpoint of light utilization, taking the effect of the treatments into consideration.

1. High accumulation of dry matter could be observed in the case of plants grown in 16 hrs illumination and 30—15 min LDP, as well as in those transferred from short rhythm to continuous light. In these treatments the quota of the stacked membranes was around 60% from the total membranes. The partition heights calculated per unit area were also the greatest in these plasts. The total membrane-length per 1 μ^2 was of high value, around 20—30 μ (Table 2).
2. In the other group, where the efficiency of photosynthesis showed a decrease, the lamellation of the plasts as well as the total membrane lengths per unit area decreased to about the half and there was also a decrease in the quota of the partitions. The quota of unstacked membranes from the total membranes was high — 50—60% — in the 15—7.5 min LDP and almost the same result was obtained by transfer from 16 hrs illumination to 15—7.5 min rhythm, as well as by exchange of the 15—7.5 min and 30—15 min cycles.

   The slightest change could be observed in respect to the stroma lamellae, their quota from the complete membrane length merely changed on the effect of the various treatments. The degree of lamellation and the partition heights per unit area were the lowest in the 15—7.5 min cycle. On the contrary, considerable increase was detectable in the ratio of the end granal membrane (to the triple). This change could be explained by the increase in granum number and the decrease of thylakoid aggregation.

Discussion

The dry mass of the 3 weeks old plants surpassed that of the control plants in the shorter rhythm treatments. This increase in production was ensured by the more intensive growth of the tripartite leaves which appeared and developed at an earlier time-point than in the long-day illumination.

It was also striking from the dry mass measurements that the short rhythms decreased the dry mass of the older, developed primordial leaves of the bean plants, and enhanced the growth and accumulation of the young leaves.

The total dry mass production of the plants grown for 5 weeks in identical LDP was lower in the short LDP than in the 16 hrs illumination.

The decrease in dry matter accumulation could be explained by the fact that although the area of the leaves and the height of the plants increased, the stem and leaf lamella were thin, the sclerenchymaelements were few and there was higher amount of water in the leaves. Our earlier studies have also determined that the epidermal cells and the number of stoma per unit area increase on the effect of short cycles. There is negative correlation between the dry mass and the cell number (MARÓTI et al., 1981).

MARÓTI and MIHALIK (1983) connect the faster development of the young leaves and the higher cellulose/starch ratio of the leaf in the short LDP with the enhanced carbohydrate translocation.

New rhythm applied at the age of 3 weeks had hardly any effect on the growth of the older, primordial leaves, the light conditions were determinative on their growth in which they developed. Therefore prelife remains determinant throughout the course of ontogenesis.

The tripartite leaves finished their growth and developed, resp. in the new rhythm, thus they quickly accommodated to the growth rate characteristic of the new LDP.

The short LDPs enhanced the growth of the plants at young age, and the leaf gaining advantage of growth in such way developed for longer period with more moderate growth intensity when transferred to continuous light, also giving the highest value of dry mass accumulation. There were differences in the manifestation of this effect according to cycle-length. The exchange of the 30—15 min and 16—8 hrs LDPs firstly increased the dry matter accumulation of the vegetative organs, while the combination of the 15—7.5 min and 16—8 hrs LDPs was more favourable to the development of the reproductive organs, accelerating their growth and ripening.

On the basis of our results relationship was searched between the dry matter production and the chloroplast size, starch content, and structure of the inner membrane.

It was determined that in the palisade cells, the size of the plasts was in negative correlation with the degree of dry matter accumulation.

Primary starch was not found accumulated in the chloroplasts of the plants in the short rhythms.

In their survey, GIFFORD and EVANS (1981) emphasized that in the literature of the recent years 50—50 such results were found according to which photosynthesis was hindered in the leaf by assimilative end products and this was not regulated by such a simple mechanism, resp, but had more profound causes. The results of MARGÓCZI (1984) demonstrated that the soluble sugar and starch level in the maize leaves decreased on the effect of illumination of shorter rhythm. The decrease in starch level experienced in the case of shorter rhythms was in good correlation with the lower assimilative starch content found in the chloroplast.

The photosynthetic efficiency and the amount of carbohydrates showed positive correlation. The more the soluble carbohydrate in the leaf, the higher the dry mass. When short-rhythm treatment increased the dry mass of the leaves, the higher production was not based on the fact that the amount of soluble carbohydrate decreased in the dark as the result of translocation, since the dry mass was the greater there where it was found in higher amount in the leaf and where the amount of soluble sugar decreased to a smaller degree (MARÓTI and MIHALIK, 1983; MARGÓCZI, 1984).

In the short LDP the number of grana increased but the grana area ratio decreased which on the one hand was the result of the grana occupying smaller part of the plasts having larger cut surface. On the other hand, there was also a decrease in the size of the grana. Increase in stroma-plasma could be observed. The majority of the PS I. particles were found in the unstacked membranes (ARNTZEN et al., 1969). There are two possibilities for the accumulation of the single membranes: the increase in stroma lamellae and the grana terminal membrane surfaces, respectively (MARÓTI and GÁBOR, 1976). In the case of beans, in short LDPs the latter was manifest with the decrease in thylakoid aggregation.

The considerable increase in the amount of grana standing of few thylakoids could be explained by the fact that due to the short and frequent dark periods the

cation/proton ratio in the stroma plasma and the intrathylakoidal spaces frequently changed and was divergent from the continuous light, resp.

It has been demonstrated (MARÓTI, 1982) that in the case of plants where besides strong illumination the value around pH 5 forms slower in the loculus, it is firstly the pigments (chlorophyll-b, neoxanthin) of the light-harvesting complexes (LHC) which become decomposed. The degree of stacking and the amount of LHC and chlorophyll-b, respectively, are in positive correlation (GEROLA, 1981; LICHTENTHALLER et al., 1981).

On the basis of the above mentonied things it is presumed that one of the important regulators of the degree of thylakoid aggregation is the exchange of H^+/Mg^{2+} between the two sides of the thylakoid membrane. Several authors have shown that photosynthesis is hindered by the decrease in stroma Mg^{2+} and pH (LATRA and KELLY, 1978; WERDAN et al., 1975).

In short LDP the low light intensity (32 W/m²) and the frequent dark periods hinder the formation of pH gradient necessary for the gaining of energy of the thylakoids. It is presumed that this is why the thylakoids become swollen and the stroma relatively acidify, resp.

It is known that ATP formation strongly depends on the pH, its maximum being at pH 8.3 (CHERYL and GOULD, 1980).

In our experiments the considerable amount of dry matter found in the case of LDPs favourable to growth was accompanied by the high value of the stacked membranes (Fig. 4). The correlation coefficient value was 0.81 which was significant at $P=1\%$.

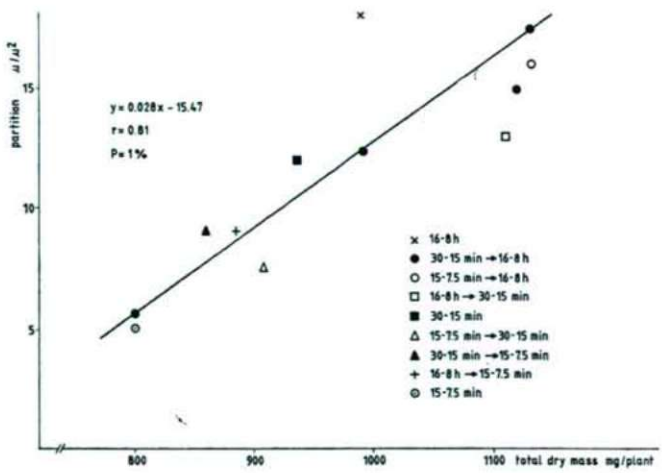

Fig. 4. Correlation between the total dry mass and stacked membrane lengths per unit area.

The changes in grana area-ratio and dry mass were nearly similar, however, no tight positive correlation was found between them (Fig. 1).

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THE SPATIAL DISTRIBUTION OF CARBOHYDRATES IN THE LEAVES OF MAIZE GROWN IN VARIOUS LIGHT-DARK CYCLES

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Abstract

The distribution of soluble sugar and starch contents was studied according to leaf stages in the leaves of 36 day old maize. The carbohydrate content of plants grown in 16 hr light and 8 hr dark (16—8 hr LDC) control illumination was compared to the values of plants grown in 30—15 min and 15—7.5 min short LDC-s. The changes in the dry mass of the plants were also evaluated.

Adaptation to the short LDC-s manifested in the decrease of the root-leaf dry mass ratio, probably corresponds to the increase in the ratio of the starch per soluble sugar content of the leaves. From the leaf stages, in the short LDCs the dry mass of the 1st and 2nd leaf, and in the 30—15 min LDC even the starch content, increased compared to the control 16—8 hr LDC.

The dry mass of the developed, still intensively photosynthesizing 3rd and 4th leaf was lower in the short LDCs. The considerable decrease observed in the carbohydrate content of these leaves may be in connection with the fact that these leaves have great role in the photosynthetic supply of the youngest 6th leaf, thus the dry mass of the 6th leaf even slightly increases in the short LDC-s and even its carbohydrate content decreases only to a little extent.

The water soluble sugar content of the less photosynthesizing part of the 4th leaf: the midrib and the leaf sheath showed considerable decrease in the short LDC, therefore this is presumably the depository which most likely becomes empty in the case of deficient photosynthate supply.

No difference in soluble sugar content was seen between the base and apex of the leaf lamina, however, the starch content of the leaf base was higher than that of the leaf apex. Difference between these lef parts were not observable on the effect of the short LDC-s.

Key words: water soluble sugar and starch content, short LDC, distribution of carbohydrates maize, leaf stages, leaf parts.

Introduction

One of the important modes of adaptation of plants to changing environmental conditions is the modification of the distribution of the primary products of photosynthesis, the carbohydrates, within the plants, as well as the transformation of the proportional ratio of the various carbohydrate forms (sugar, starch, cellulose).

SCHULZE et al. (1983) studied the increase in biomass of *Vigna unguiculata* plants using the method of mathematical modelling. They have determined that the balance of the growth of the shoot and the root is attained through the changes of the carbohydrate partitioning namely in the function of transpiration and the water absorb capacity of the root.

During the course of adaptation to weaker light intensity the partition into shoots of the photosynthates becomes intensified and thus the shoot/root dry mass ratio, i.e. the ratio of the photosynthesizing/non-photosynthesizing organs increases (BJÖRKMAN, 1982).

On the basis of the studies by CHATTERTON and SILVIUS (1980) the length of the light period also influences the accumulation of photosynthetic starch in the leaf: in the case of shorter light period the accumulation is of higher degree. The distribution of carbohydrates is further influenced not only by the environmental factors but also by the internal demands of the plant which change during the course of ontogenesis. For example, the growth rate of the intensively growing so-called "sink" leaves have influence the carbohydrate level of the older, so-called "source" leaves feeding them (BARLAW and BOERSMA, 1976).

At the time of crop formation the increased photosynthate demand causes the increase of starch accumulation in daylight and its mobilization at night in the photosynthesizing leaves (HAMMOND and BURTON, 1983).

Therefore, the accumulation of photosynthetic starch in the leaf does not serve as the storer of excessive carbon, but it is regulated by complicated control mechanisms according to the demands of the plant and the changes of the environment (HUBER, 1983).

The light-dark cycles varying from thet natural are generally unfavourable to the development of the plant and the increase in dry matter (SAGER and GIGER, 1980), i.e. they mean considerable stress on the plant. Nevertheless there are such period lengths also, where — at least in the case of certain plant species — increase in dry mass is observable in the case of identical daily amount of light compared to light-dark cycles (LDC-s) of natural length (GARNER and ALLARD, 1931; GAUDILLIÉRE, 1977; HORVÁTH et al., 1977; MARÓTI and MIHALIK, 1983).

Adaptation to short light-dark cycles can be expected in the changes of carbohydrate distribution, partly in the changes regarding the ratio of soluble sugars and starch compared to each other, as well as in the changes in the distribution of carbohydrates between leaves of various ages and also in the different parts of one particular leaf.

Based on earlier studies, the soluble sugar, starch and cellulose contents of the 5th leaves (counted from the bottom of 5-week-old maize) were enhanced or reduced depending on genotype in the 30—15 min. LDC. The 15—7,5 min LDC, however, strongly decreased the soluble sugar and starch contents of the 4th and 5th leaves in the case of every genotype, while the cellulose content [$\mu g\ mg^{-1}$] was increased (dry mass, mg/leaf) (MARÓTI and MIHALIK, 1983). We have no data on how the carbohydrate content of the older (1st—3rd) and the youngest (6th) leaves changes compared to the central leaves, furthermore, on how the carbohydrate content changes on the effect of short LDCs in the various parts of one single leaf. The relationship between the changes observed in carbohydrate content and dry mass of the plant organs is still to be studied. In the present paper answer is sought to the above questions studying 36 days old individuals of P3732 and P3839 hybrid maize.

Materials and Methods

In our experiments 3732 and 3839 Pioneer maize hybrids were used. The maize grains were sown in the mixture of washed sand-perlite in the ratio of 1:1. The moisture and nutriment content of the growing medium was ensured by mixture with Hoagland nutrient solution (REYSS and BOURDU, 1971) modified by BÉRCZI et al. (1982) and MARÓTI. The macroelement content of the nutrient solution was as follows: K^+ (3 mM), Na^+ (0.4 mM), Ca^{2+} (5 mM), Mg^{2+} (0.4 mM), NO_3^- (12 mM) Cl^- (1 mM), HPO_4^{2+} (0.2 mM), SO_4^{2-} (0.4 mM) per dm^3. The microelement content was: BO_3^{3-}

(1.6 mM), Mn^{2+} (0.8 mM), MoO_4^{2-} (0.05 mM), Zn^{2+} (21.8 μM), Cu^{2+} (25.1 μM) per dm^3. The moisture content of the medium was set to the value of water capacity corresponding to 80%. The original moisture content was maintained daily with tap water by watering according to weight. The pH ranged from 7.4 and 8.2 in the medium.

In a plastic pot with volume of 600 cm^3 5 maize grains were sown 4—5 cm deep. At the age of two weeks the plant numbers were changed to 3 per dish. Nutriment was supplied twice a week: with 20 ml of above described nutrient solution per pot. The plants were grown in phytotron (HORVÁTH, 1972). In the climate chambers the temperature was 21 ± 2 °C, the relative moisture content of the air was 50—70%. The CO_2 concentration was kept on the same level by constant mixing with fresh air. F29 and F33 light tubes were used for illumination. The strength of illumination in the light phase was 32 Wm^{-2} (= 185 $\mu Em^{-2}s^{-1}$).

Three kinds of light treatment were applied: The alternation of 16 hours light and 8 hours dark was used in the first climate chamber (16—8 hr LDC). The light phase lasted from 8 a.m. till midnight. In the second climate chamber 30 min light and 15 min dark (30—15 min LDC) and in the third 15 min light and 7.5 min dark (15—7.5 min LDC) alterated continuously.

The duration of the daily total illumination was 16 hours in all three chambers, thus the daily total radiating energy was 1843 kJm^{-2}.

Two experiments were carried out: the individual number was 15 per chamber in the first and 9 in the second.

The carbohydrate content was determined on 9—9 plants from the second experiment.

The plants were processed at the age of 36 days, during the hours before noon. From the short LDC-s the samples were taken during the light phase according to organs and leaf stages. The separated plant matter taken from the 4th leaf of the P3839 hybrid according to leaf parts (leaf base — centre — apex) was fixed at 105 °C for 5 min and then dried for 10 days at 60 °C. Then dry mass was measured on analytical scale. The carbohydrate content was determined from the pulverized dry matter. The soluble sugar was extracted twice with hot water. The starch was extracted from the sediment with perchloric acid according to the method of MCCREADY et al. (1950). The sugar content of the extracts was measured with the phenol-sulphuric acid method of DUBOIS et al. (1956) and determined with the aid of comparative solution prepared from glucose from the extinction values. (For detailed description of the method see: MARÓTI and MARGÓCZI, 1984).

The results were statistically evaluated: the significance of the variations in values obtained from the 16—8 hours control LDC and the two short LDC-s was determined with the help of the t-probe. In the Tables and graphs the significance appears as follows: P = 10%*, P = 5%**, P = 1%***, P = 0.1%****.

Results

1. THE EFFECT OF SHORT LDCs ON THE DRY MASS OF 36 DAYS OLD MAIZE PLANTS

In 3732 hybrid maize the dry mass of each organ decreased on the effect of short LDCs at the age of 5 weeks. The total dry mass showed a decrease in the 30—15 min LDC compared to the 16—8 hr LDC, and even further decrease was experienced in the 15—7,5 min LDC (Table I).

Table I. Dry mass of the various organs of P3732 hybrid maize at the age of 36 days in normal and short LDCs [mg/plant], and the proportional quota of the organs from the total dry mass. The data are the average values of 24 plants. The significance of the variation from the values of the 16—8 hr LDC is demonstrated according to the description in Materials and Methods.

LDC	Dry mass							
	root		leaf sheath		leaf lamella		total	
	mg	%	mg	%	mg	%	mg	%
16—8 hour	657.8 *	46.9	246.6	17.6	497.4	35.5	1402.0	100
30—15 min	504.1 ***	45.0	160.7 *	15.2	446.5	39.8	1111.3	100
15—7.5 min	431.9	41.9	181.6	17.6	418.2	40.5	1031.6	100

The dry mass decreasing effect of the short LDCs was of various degree in the organs of the plants. The dry mass decreased the most in the root, and the least in the leaf, therefore the organ-ratios changed in the short LDCs. The quota of the dry mass in the root decreased from the total dry mass and that of the leaf showed an increase (Table I).

The length of the leaf sheaths increased in the short LDC, but their thickness decreased. (In the 36 day old plants the leaf sheaths play role as the stem. The initiatives of the young leaves are protected by the cob formed by the older leaf sheaths. In our paper this stem-like organ: the initiatives of the young leaves and the older leaf sheaths protecting them, are jointly named as the leaf sheath). Due to the two kinds of proportion changes, in the 30—15 min LDC the decrease in dry mass of the leaf sheaths refers to the fact that the decrease in thickness prevails in this part of the plant, while in the 15—7.5 min LDC, due to the organ's vigorous increase in length, its dry mass decreased less as in the 30—15 min LDC, and its quota from the total dry mass is the same as in the control 16—8 hr LDC.

2. Changes in dry mass of the leaf stages in short LDC

At the time of harvesting the plants were in six-leaved state. The 1st, lowest leaf was strongly dry, the 2nd leaf was less dry. The lingule of the 3rd and 4th leaves already appeared, therefore they were considered to be completely developed leaves. The 5th leaf was of significant size, but was still intensively growing. The 6th leaf appeared 3—5 cm from the cob formed by the leaf sheaths. (Dry mass measurement and carbohydrate determination were only performed from this 3—5 cm part).

During the course of the experiments it was observed that the lingule of the leaves appeared 1—1.5 days earlier in the short LDCs than in the control 16—18 h LDC. In the short LDCs the degree of withering was lower in the case of older leaves. The short LDCs had various effects on the different aged leaves of the plants. In the 30—15 min LDC the increase in dry mass of the 1st and 2nd leaves reached 20% compared to the control 16—8 h LDC, but in the 15—7.5 min LDC it was also 10% (Table 2). In both short LDCs the dry mass of the 3rd, 4th and 5th leaves decreased; strongly that of the 4th leaf, less that of the 3rd and 5th leaves. The dry mass of the 6th, youngest leaf only slightly increased in the short LDCs (Table 2).

Table II. Dry mass of the leaf lamellae of P3732 hybrid maize at the age of 36 days in normal and short LDCs [mg/leaf]. The leaf stages were counted from the bottom. The data represent the averages of 24 plants

LDC	Dry mass [mg/leaf]						
	Leaf position	1.	2.	3.	4.	5.	6.
16—8 hour		13.2	34.0	92.2	179.0	139.3	39.6
30—15 min		15.9	41.4	82.5	137.9	127.6	41.6
15—7.5 min		14.4	37.2	74.1	126.4	126.0	40.1

3. Carbohydrate content of the leaves

3.1. *The water soluble sugar content* (Fig. 1):

In the 16—8 hr LDC the water soluble sugar content of the leaves referring to dry mass unit developed as follows: it was found to be relatively high in the old 1st and

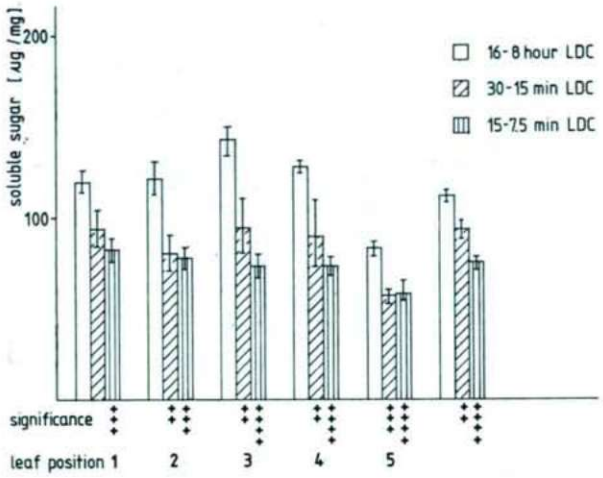

Fig. 1. The development of the water soluble sugar content in each leaf stage of P3732 hybrid maize in control and short LDCs, referred to dry mass unit (μgmg^{-1}). The data are the average values of 9—9 35 days old plants. The significance of the variation from the data of the 16—8 hr control LDC is demonstrated according to the description in Materials and Methods. The leaves counted from the bottom upwards.

2nd leaves, and was the highest in the developed 3rd and 4th leaves. Strikingly low amount of water soluble sugar was found in the 5th leaf — growing intensively, but already having larger area than the 4th leaf — and again somewhat higher amount was found in the 6th leaf. The difference in water soluble sugar content between the leaf stages became moderate in the short LDC. These differences almost disappeared in the 15—7.5 min LDC, only the low soluble sugar level of the 5th leaf was striking. More or less equal amount of water soluble sugar was found in the rest of the leaves, per unit dry mass.

3.2. *Starch content* (Fig. 2):

In the 16—8 hr LDC the starch level referring to dry mass unit was similarly high in the 4th, 5th and 6th leaves. It was rather low in the old, 1st leaf, and in the 2nd and 3rd leaves the starch content was found to be between the two above mentioned values. Namely, the starch level increased from the 1st to the 4st leaf. The starch level of the leaf stages compared to each other showed strong modification in the 30—15 min LDC: that of the 1st leaf was also relatively low here, but was still higher than the equivalent data of the 16—8 hr LDC.

The starch level of the 2nd leaf was strikingly high, from here it decreased till the 3rd, 4th leaves, increasing again in the 5th and 6th leaves.

Similar tendency was observed in the 15—7.5 min LDC with the difference that here an increase in starch level could not be experienced even in the 1st and 2nd leaves compared to the adequate data of the 16—8 hr LDC.

As a summary therefore, it could be concluded that the short LDCs only decreased the soluble sugar content of the lower 1st and 2nd leaves, the starch content even increased in these leaves on the effect of the 30—15 min LDC. Both the water soluble sugar and starch levels strongly decreased in the 3rd and 4rd leaves. In the

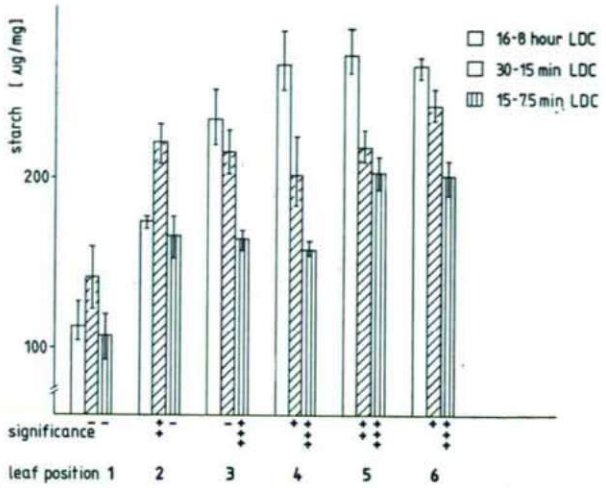

Fig. 2. The development of the starch content in each leaf stage of P3732 hybrid maize in control and short LDCs, referred to dry mass unit (μgmg^{-1}). The data are the average values of 9—9 35 days old pants. The significance of the variation from the data of the 16—8 hr control LDC is shown according to the description in Materials and Methods. The leaves were counted from the bottom upwards.

5th leaf the decrease was somewhat slighter and in the 6th leaf the decrease of carbohydrate content was even more moderate in short LDC.

Studying the percental share of starch from the total carbohydrate content, a continuous increase in starch proportion could be observed from the older leaves to the younger ones in each LDC, with the exception of the youngest leaves where the proportion of starch was found to be lower than in the previous leaf stages (Table 3).

Table III. The carbohydrate content referring to dry mass unit of the leaf lamellae of P3732 hybrid maize: water soluble sugar+starch: Su+St [µg/mg] and the quota of starch from the total carbohydrate content: St%. The data are the averages of 9—9 plants. The leaf stages were counted from the bottom.

LDC		Leaf position					
		1.	2.	3.	4.	5.	6.
16—8 hour	Su+St [µg/mg]	233.1	296.3	376.2	393.3	355.6	376.8
	St%	48.7	58.9	62.2	67.6	76.6	70.5
30—15 min	Su+St [µg/mg]	244.9	300.3	309.6	290.9	275.9	335.8
	St%	61.9	73.5	69.5	69.3	79.2	72.1
15—7.5 min	Su+St [µg/mg]	189.9	244.2	238.4	249.9	261.5	274.6
	St%	56.6	68.1	69.1	71.2	78.8	73.0

Comparing the effect of the various LDC treatments for each leaf stage, it could be seen that the proportion of starch always increased in the short LDCs. In general, there were no great differences in this regard between the two short LDCs (Table 3).

4. The carbohydrate content in the various parts of the 4th leaf (Figs. 3—4)

This experiment was carried out on the 4th, leaf of 36 days old P3839 hybrid maize plants. The carbohydrate content per dry mass unit was determined separately in the leaf sheath, midrib and the base, center and apex of the leaf lamella. The results showed that in the 16—8 hr LDC there were no differences between the various

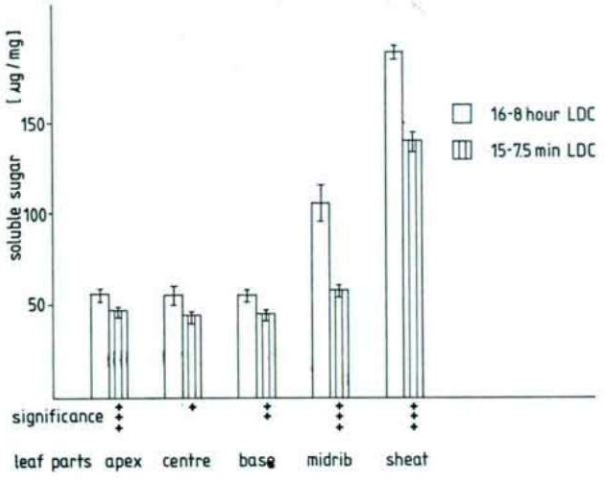

Fig. 3. The development of the soluble sugar content in the various parts of the 4. leaf of P3839 hybrid maize in 16—8 hr and 15—7.5 min LDCs, referred to dry mass unit (μgmg^{-1}). The data are the average values of 9—9 35 days old plants. The significance of the variation from the data of the 16—8 hr LDC is demonstrated according to the description in Materias and Methods.

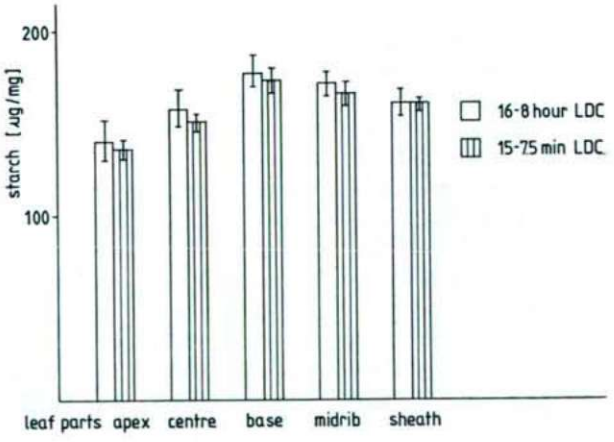

Fig. 4. The development of the starch content in the various parts of the 4. leaf of P3839 hybrid maize in 16—8 hr and 15—7.5 min LDCs, referred to dry mass unit (μgmg^{-1}). The data are the average values of 9—9 35 days old plants. The variations from the data of the 16—8 hr LDC did not prove to be significant in this experiment.

parts of the leaf lamella in respect to the soluble sugar content. The soluble sugar content of the midrib was almost the double of the sugar content of the leaf lamella and that of the leaf sheath was even higher (Fig. 3). On the effect of 15—7.5 min LDC the soluble sugar level of the leaf lamella only slightly decreased, however, the decrease was about 40% in the midrib, and 25% in the leaf sheath. In the leaf lamella the starch content increased from the apex to the base both in the 16—8 hr and 15—7.5 min LDCs. The starch content was considerable in the midrib and sheath of the leaf. On the effect of short LDC the starch content decreased slightly but not significantly in the various parts of the leaf lamella and in the midrib, but showed no changes in the leaf sheath (Fig. 4).

Discussion

Since both the dry mass and carbohydrate content/dry mass unit of the plants decreased (Tables 1, 3) it could be concluded that in short LDCs there is a decrease in the daily gain of CO_2, i.e. in the net photosynthesis. Though in the short LDCs the plants received the same amount of daily light (1843 kJm^{-2}) as in the 16—8 h control LDC, the repeated, compulsory adaptation due to the frequent light-dark-light transition in the short LDCs hinders the more complete utilization of the light. That is, the plants "starve" in the short LDCs, the same amount of light used in short periods seems to be less for the plant, being less able to utilize it in the formation of carbohydrate. Therefore, it is compelled to ensure the relatively optimal growth by modifying the distribution of the photosynthates as described in the followings.

On the one hand the ratio of the photosynthesizing and nonphotosynthesizing organs changes to the benefit of the photosynthesizing leaves (Table 1). This was also concluded by BJÖRKMAN (1982) in the case of applying weaker light intensity compared to the stronger one.

Regarding the modification of the organ-ratio, such a mechanism may play role which is effective on the growth of the root through influencing the starch level of the leaf. In our case the decrease in the root proportion observed in the short LDCs may be in relationship with the increase in the ratio of starch/soluble sugar. This assumption is in conformity with the results of HUBER (1983), who found connection between the higher starch/sugar ratio and the lower root/shoot dry mass ratio of the leaf in plants having various genotype and nitrogen supply.

The changes in phosphoglyceric acid and inorganic phosphate level of the chloroplast — through the phosphate translocator — may possibly play role in the regulation (WALKER, 1976; PREISS, 1982).

The photosynthetic starch accumulation-reducing effect of the plant's temporary increased photosynthate demand — which appears in the greater saccharose translocation — is realized through this system. However, not every link has been clarified as yet regarding the path leading from the changes of environmental factors to the accommodation the biochemical metabolism of the cell. The temporary photosynthate demand is probably not the only influencing element of the photosynthetic starch accumulation, as in such case the lower starch/sugar ratio of the leaf should have been found in the short LDCs.

In our experiment the leaves of various ages behaved differently on the effect of short LDC.

The dry mass of the lower (1st, 2nd) leaves was found to be higher in both short LDCs than in the control LDC (Table 2), and the starch content was also higher in the 30—15 min LDC (Fig. 2). These leaves developed when the reserve nutriment of the germinating seed still strongly contributed to the development of the plant, i.e. the nutriment flow from the seed probably compensated the decreased CO_2 gain in the short LDC. It is of interest that the high starch content observed in the 1st ans 2nd leaves in the 30—15 min LDC refers to the fact that these leaves did not even completely "empty" at the time when newer leaves grew.

In all probability the considerable decrease in the soluble sugar and starch content of the no longer growing, but still intensively photosynthesizing 3rd and 4th leaves makes it possible that the dry mass of the 6th leaf even increases to a certain extent in the short LDC, and the carbohydrate content only slightly dec reases (Table 3). This observation is in accord with the results of BARLAW and BOERSMA (1983), according to whom there is relationship between the growth rate of the young leaves and the carbohydrate level of the older leaves feeding them.

Similarly to the results of MILFORD and PEARMAN (1975), CHANG (1979), and POTTER (1980), in our experiment it was found that the proportion of starch was higher in the total extracted carbohydrate in the younger leaves than in the older ones (Table 3).

Since the short LDC increases the proportion of starch at identical leaf stages (Table 3), we can presume that this also means the retardation of the aging the leaf. This is further referred to by our observation that in the short LDC the lower leaves wither later than in the 16—8 hr LDC.

On studying the carbohydrate content of the leaf parts it was determined that the proportion of starch decreases from the base towards the apex (Fig. 3, 4). The differences in age of the three leaf parts are presumably reflected in this: the basal part is the youngest, the leaf apex is older. PERCHOROWICZ and GIBBS (1980) found difference between the basal and apex parts of maize leaves regarding the explicity of the C4 features. The carbohydrate content in all three parts of the leaf lamella decreases to the same extent on the effect of short LDC (despite the differences in age). Compared to the photosynthesizing part of the leaf lamella rather considerable decrease can be observed in the soluble sugar content the midrib of the leaf and leaf sheath on the effect of short LDC. This may refer to the fact that the depository best available for the younger leaves in case of deficient photosynthate supply is firstly the soluble carbohydrate content of the less photosynthetic part of the 4th leaf, having main role in the photosynthate supply of the young leaves.

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ÉTUDE PALYNOLOGIQUE D'UN LIGNITE TERTIAIRE DE BLAO, VIET-NAM -II-

M. KEDVES

(Reçu, le 5 janvier 1983)

Fgen: *Tricolpites* (ERDTMAN 1947, COOKSON 1947, ROSS 1949, COUPER 1953) emend. R. POT. 1960

1. Tricolpites blaoensis n. fsp. (Planche IV, fig. 1—4)

Diagnose

Contour triangulaire à coins convexes, ou circulaire. Surface très finement réticulée. La maille des réticulations n'atteint jamais 0,5 μm. L'exine est très mince, sa structure n'est pas bien visible au microscope optique; l'épaisseur n'atteint pas 0,5 μm. Les sillons sont très courts.
Plus grande dimension: 25—35 μm.
Holotype: Planche IV, fig. 1, 2, prep. Blao-8; 8,3/106,3.
Derivatio nominis: de la localité type.
Diagnose différentielle: le *Tricolpites pannosus* DETTMANN et PLAYFORD 1968 est scabre, comparé à notre espèce de forme nouvelle.
Appartenance botanique probable: *Dicotyledonopsida.*

Fgen: *Bombacacidites* COUPER 1960

1. *Bombacacidites vancampoae* n. fsp. (Planche IV, fig. 5,6)

Diagnose

Contour triangulaire, côtés convexes, les apertures situées au milieu des côtés. Surface réticulée. La maille des réticulations aux angles mesure de 1,5 à 2,5 μm, et dans la région polaire de 3 à 4,5 μm. L'exine est épaisse de 1,5 à 2 μm. Les sillons sont courts, de 6 à 10 μm. Autour des sillons il y a une épaississement de 2,5 μm de largeur environ.
Plus grande dimension: 40—50 μm.
Holotype: Plache IV, fig. 5,6, prep. Blao-8; 17,7/110,0.
Derivatio nominis: en hommage à MME. M. VAN CAMPO, directeur du Laboratoire de Palynologie, Montpellier.
Diagnose différentielle: la taille, plus grande, et l'épaississement autour des sillons séparent cette espèce du *B. zaklinskaiae* KDS. 1974. Le diamètre de *B. nacimientoensis* (ANDERS. 1960) ELSIK 1968 de 35 à 39 μm.
Appartenance botanique probable: *Bombacaceae.*

Fgen: *Saurinipollenites* n. fgen.
Fgen. type: *Saurinipollenites circulus* n. fsp. (Planche IV, fig. 7,8)

Diagnose

Contour circulaire. Surface lisse ou scabre. Structure intrabaculée. Les apertures germinales sont des sillons courts, leurs longueur n'atteint jamais le 1/3 du rayon du pollen.

Fgen. type: Planche IV, fig. 7,8, prep. Blao-11; 14,3/103,9.
Derivatio nominis: en hommage à MONS. LE PROFESSEUR SAURIN.
Diagnose différentielle: la surface lisse distingue bien ce genre du genre de forme *Bombacacidites* COUPER 1960, et du *Intratriporopollenites* TH. et PF. 1953.

1. *Saurinipollenites circulus* n. fsp. (Planche IV, fig. 7,8)

Diagnose

Contour circulaire, surface lisse ou scabre. L'exine est épaisse de 2—2,3 μm, le tectum et la sole sont très minces. Structure intrabaculée, les éléments de la sculpture sont nets et quelquefois se ramifient. Les sillons ont 10—12 μm de long. Autour des sillons il y a aucun différenciation de l'exine.
Plus grande dimension: 30—40 μm.
Holotype, voir chez le genre de forme.
Derivatio nominis: du contour circulaire.
Appartenance botanique probable: *Dicotyledonopsida.*

Fgen: Incertae
Forme réticulée (Planche IV, fig. 9,10)

Nous avons trouvé une seule exemplaire. Il possede un sillon, avec un endopore allongé en sillon transversal. L'épaisseur de l'exine de 2 à 3 μm; parmi les couches de l'ectexine l'infratectum est la plus épaisse. La maille des réticulations de 1,5 à 2,5 μm. Plus grande dimension: 43 μm.

Fgen: *Retitricolpites* (VAN DER HAMMEN 1956) VAN DER HAMMEN et WIJMSTRA 1964

1. Cf. *Retitricolpites* fsp. (Planche IV, fig. 11,12)
2. *Retitricolpites guinetii* n. fsp. (Planche IV, fig. 13,14)

Diagnose

Contour elliptique. L'épaisseur de l'exine est de 2 μm environ, l'infratectum constitue la couche la plus épaisse parmi les couches de l'ectexine. Les sillons n'atteignent pas toujours les pôles, l'un d'eux est plus court que les deux autres. Surface réticulée. La réticulation autour des sillons est fine, les mailles sont toujours inférieures à 0,5 μm. Dans la région extragerminale, la maille mesure de 2 à 3 μm environ.
Plus grande dimension: 43—55 μm.
Holotype: Planche IV, fig. 13,14, prep. Blao-12; 7,3/105,8.
Derivatio nominis: en hommage à MONS. PH. GUINET.
Diagnose différentielle: la taille relativement grande sépare nettement cette espèces des autres de ce genre de forme.
Appartenance botanique probable: *Tiliaceae.*

3. *Retitricolpites blaoensis* n. fsp. (Planche IV, fig. 15,16)

Diagnose

Contour elliptique. Parmi les sillons, deux atteignent les pôles, ou se ramifient, le troisième n'atteint jamais les pôles. Autour des sillons il y a des amincissements. La maille du réseau est de 1,5 à 2 µm; leurs diamètre n'est pas réduit autour des sillons. L'épaisseur de l'exine est de 1,3 µm environ et les trois couches de l'ectexine ont la même épaisseur.
Plus grande dimension: 28—33 µm.
Holotype: Planche IV, fig. 15,16, prep. Blao-4; 14,6/110,3.
Derivatio nominis: de la localité type.
Diagnose différentielle: la taille, plus petite, et la réticulation, qui est identique dans les régions germinale et extragerminale distingue nettement cette espèce de l'espèce de forme précédente.
Appartenance botanique probable: *Hamamelidaceae, Corylopsis* (WANG et al. 1960).

4. *Retitricolpites vancampoae* n. fsp. (Planche IV, fig. 17,18)

Diagnose

Contour elliptique. Les sillons n'atteignent pas les pôles. Autour des sillons il n'y a pas d'amincissement. L'épaisseur de l'exine est de 2 à 3 µm environ, la couche infratectale est plus épaisse que le tectum et la sole. La maille des réticulations est de 0,3 à 0,5 µm, les murs sont étroits, de 0,2 µm environ.
Plus grande dimension: 28—36 µm.
Holotype: Planche IV, fig. 17,18, prep. Blao-17; 10,2/114,8.
Derivatio nominis: en hommage à MME. M. VAN CAMPO.
Diagnose différentielle: la réticulation plus fine distingue bien cette espèce de *R. blaoensis* n. fsp.
Appartenance botanique probable: cf. *Salicaceae*.

5. *Retitricolpites saurinii* n. fsp. (Planche IV, fig. 19,20)

Diagnose

Contour elliptique. L'exine est épaisse d'environ 1 µm, les trois couches de l'ectexine ont la même épaisseur. Les sillons sont relativement courts. La réticulation est extrémement fine, la maille des réticulations et la largeur des murs sont d'environ 0,1 µm.
Plus grande dimension: 25—30 µm.
Holotype: Planche IV, fig. 19,20, prep. Blao-19; 12,6/112,5.
Derivatio nominis: en hommage à MONS. LE PROFESSEUR SAURIN.
Diagnose différentielle: l'exine mince distingue nettement des autres espèces de ce genre de forme.
Appartenance botanique probable: *Leguminosae, Smithia* (HUANG 1972).

6. *Retitricolpites crassiexinus* n. fsp. (Planche IV, fig. 21,22)

Diagnose

Contour elliptique. L'exine atteint 2 à 3 µm d'épaisseur. Parmi les couches de l'ectexine, la couche infratectale est la plus épaisse. La sculpture réticulée est très fine. La maille du réseau, et la largeur des murs sont de 0,1 µm environ.

Plus grande dimension: 33—40 µm.
Holotype: Planche IV, fig. 21,22, prep. Blao-3; 12,3/111,2.
Derivatio nominis: de l'exine rélativement épaisse.
Diagnose différentielle: l'exine, rélativement épaisse, et la réticulation fine distinguent bien cette espèce de *R. guinetii* n. fsp.
Appartenance botanique probable: *Dicotyledonopsida.*

Fgen.: *Cupuliferoipollenites* R. POT. 1960 non 1951

1. *Cupuliferoipollenites oviformis* (R. POT. 1931) R. POT. 1960, *Fagaceae, Castanea* (Planche IV, fig. 23,24)

2. *Cupuliferoipollenites pusillus* (R. POT. 1934) R. POT. 1960, *Fagaceae,* cf. *Castanea* (Planche IV, fig. 25—30)

Fgen.: *Fususpollenites* KDS. 1978

1. *Fususpollenites fusus* (R. POT. 1931) KDS. 1978, *Fagaceae, Castanopsis.* Suivant HUANG (1972) le genre *Lithocarpus* peut aussi entrer en ligne de compte (Planche IV, fig. 31—34)

Fgen.: *Cyrillaceaepollenites* (MÜRRIGER et PFLUG 1951) R. POT. 1960

1. *Cyrillaceaepollenites exactus* (R. POT. 1931) R. POT.1960, *Cyrillaceae, Clethraceae* v. *Theaceae* (Planche IV, fig. 35—40). Suivant HUANG (1972), la famille des *Elaeocarpaceae* possede un type pollinique voisin.

Fgen.: *Psilatricolporites* (VAN DER HAMMEN 1956) VAN DER HAMMEN et WIJMSTRA 1964

1. *Psilatricolporites* cf. *laevigatoides* KDS. 1978, cf. *Fabaceae,* suivant WANG et al. (1960) le genre *Campylotropis* est probable (Planche IV, fig. 41,42)

2. *Psilatricolporites asiaticus* n. fsp. (Planche IV, fig. 43,44)

Diagnose

Contour circulaire, surface lisse. L'épaisseur de l'exine est de 1,5 à 2 µm; les trois couches de l'ectexine sont égales. Les sillons sont très minces et courts, n'atteignent jamais les pôles. Autour des sillons il y a une interscription de l'exine de 2 µm de largeur. L'endopore est de forme circulaire, relativement grand, de 3 à 4 µm de diamètre.
Plus grande dimension: 18—25 µm.
Holotype: Planche IV, fig. 43,44, prep. Blao-14; 13,1/104,6.
Derivatio nominis: de l'Asie.
Diagnose différentielle: c'est la forme en premier lieu qui distingue bien cette espèce des autres espèces de forme décrites. *P. globus* (DEÁK 1960) KDS. 1978 est plus grand. Les endoapertures du *P. psilatus* ROCHE et SCHULER 1976 sont des pores elliptiques. *P. calabarensis* JAN DU CHÈNE, ONYIKE et SOWUNMI 1978 est plus grande, que l'espèce de forme nouvelle.
Appartenance botanique probable: *Dicotyledonopsida.*

Fgen.: *Intrabaculitricolporites* KDS. 1978

1. *Intrabaculitricolporites vancampoae* n. fsp. (Planche V, fig. 13, 14)

Diagnose

Contour elliptique. Surface finement granuleuse. L'épaisseur de l'exine est de 2 µm environ. La sole est la couche la plus épaisse parmi les couches de l'exine.

Structure très finement intrabaculée. Les sillons atteignent les pôles. Autour des sillons il y a un amincissement de 1 µm largueur environ. Les endopores sont circulaires de 2 µm de diamètre.
Plus grande dimension: 18—23 µm.
Holotype: Planche V, fig. 13, 14, prep. Blao-15; 6,3/117,3.
Derivatio nominis: en hommage à Mme. M. Van Campo.
Diagnose différentielle: la forme de l'endopore distingue bien cette espèce de *I. pokrovskaiae* Kds. 1978.
Appartenance botanique probable: *Dicotyledonopsida.*

2. *Intrabaculitricolporites guinetii* n. fsp. (Planche V, fig. 15, 16)

Diagnose

Contour elliptique. Surface finement granuleuse. L'épaisseur de l'exine est de 2,5 µm environ. La sole est la plus épaisse parmi les couches de l'ectexine. Structure très finement intrabaculée. Les sillons sont longs, mais n'atteignent pas toujours les pôles. Les amincissements ont de 2 à 3 µm de large. L'endopore est circulaire, de 2,5 à 3 µm de diamètre.
Plus grande dimension: 20—30 µm.
Holotype: Planche V, fig. 15, 16, prep. Blao-18; 6,4/109,8.
Derivatio nominis: en hommage à Mons. Ph. Guinet.
Diagnose différentielle: les endopores, plus grands, et les sillons relativement courts distinguent bien cette espèce de *I. vancampoae* n. fsp.

Fgen.: *Granotricolporites* Kds. 1978

1. *Granotricolporites minor* n. fsp. (Planche IV, fig. 45—50)

Diagnose

Contour elliptique. Surface très finement granuleuse. Les sillons sont relativement longs, atteignent les pôles, ou fusionnent. L'amincissement est de 1 µm de large. L'épaisseur de l'exine de 1,5 à 2 µm, les trois couches de l'ectexine sont égales. La structure de la couche infratectale n'est pas distincte au microscope optique. Les endopores sont circulaires, de 1,5 µm de diamètre environ.
Plus grande dimension: 16—20 µm.
Holotype: Planche IV, fig. 49, 50, prep. Blao-18; 9,4/116,7.
Derivatio nominis: de la taille petite de ces pollens.
Diagnose différentielle: la taille relativement minuscule par rapport aux autres espèces distingue bien notre espèce de forme nouvelle décrite.
Appartenance botanique probable: *Dicotyledonopsida.*

2. *Granotricolporites asiaticus* n. fsp. (Planche V, fig. 1, 2)

Diagnose

Contour elliptique. Surface finement granuleuse. L'épaisseur de l'exine est de 1,2 à 1,5 µm. La couche infratectale est un peu plus épaisse que le tectum et la sole. Structure intrabaculée. Parmi les sillons il y a un, qui est plus court que les deux autres. Autour des sillons il y a un étroit amincissement. Les endoapertures ont 5 µm de long et 1,3 µm de large.

Plus grande dimension: 18—25 µm.
Holotype: Planche V, fig. 1, 2, prep. Blao-10; 13,8/116,4.
Derivatio nominis: de l'Asie.
Diagnose différentielle: les endoapertures longues permettent de distinguer cette espèce des autres espèces décrites.
Appartenance botanique probable: *Dicotyledonopsida.*

3. *Granotricolporites saurinii* n. fsp. (Planche V, fig. 3—8)

Diagnose

Contour elliptique. Surface finement granuleuse. L'épaisseur de l'exine est de 1 à 1,5 µm, les trois couches de l'ectexine sont égales. Structure intrabaculée. Les sillons sont longs, mais n'atteignent pas toujours les pôles. Autour des sillons il y a un amincissement de 1,5 à 2 µm de large. Les endopores sont circulaires, de 2—2,5 µm de diamètre.
Plus grande dimension: 17—26 µm.
Holotype: Planche V, fig. 3, 4, prep. Blao-6; 19,0/109,5.
Derivatio nominis: en hommage à MONS. LE PROFESSEUR SAURIN.
Diagnose différentielle: c'est la forme des endoapertures, qui sépare nettement cette espèce de *G. asiaticus* n. fsp.
Appartenance botanique probable: *Dicotyledonopsida.*

4. *Granotricolporites blaoensis* n. fsp. (Planche V, fig. 9—12)

Diagnose

Forme allongée. Sculpture finement granuleuse. L'épaisseur de l'exine est de 1,2 à 1,6 µm; la couche infratectale est beaucoup plus épaisse que le tectum et la sole. Structure columellaire. Les sillons atteignent en général les pôles. Autour des sillons l'amincissement de l'exine de 1,7 µm de large près des endoapertures, est plus ètroite vers les pôles les endoapertures sout de forme circulaire, de 3µm de diamètre environ.
Plus grande dimension: 23—30 µm.
Holotype: Planche V, fig. 9, 10, prep. Blao-20; 7,7/113,7.
Derivatio nominis: de Blao, de la localité type.
Diagnose différentielle: la dimension des endoapertures, et la symmétrie permettent de séparer cette espèce de *G. saurinii* n. fsp.
Appartenance botanique probable: *Dicotyledonopsida.*

5. *Granotricolporites circulus* n. fsp. (Planche V, fig. 17—20)

Diagnose

Contour de forme circulaire. Surface finement granuleuse. L'épaisseur de l'exine est d'environ 2 µm. C'est la couche infratectale qui est la plus épaisse parmi les couches de l'ectexine. Les sillons atteignent les pôles, quelquefois deux d'entre eux se rejoignent. Les amincissements sont de 1 à 2 µm de large. Les endoapertures sont longues (4 µm) et minces (1 µm), de forme irrégulière.
Plus grande dimension: 16—25 µm.

Holotype: Planche V, fig. 17, 18, prep. Blao-13; 6,4/104,1.
Derivatio nominis: de la forme du contour.
Diagnose différentielle: c'est le contour qui sépare nettement cette espèce des autres espèces de ce genre de forme.
Appartenance botanique probable: *Rosaceae* (cf. WANG et al. 1960) ou *Chrysobalanaceae.*

6. *Granotricolporites vancampoae* n. fsp. (Planche V, fig. 21—26)

Diagnose

Contour elliptique. Surface finement granuleuse. L'épaisseur de l'exine est d'environ 1,5 µm. Les trois couches de l'ectexine sont de même épaisseur. Structure finement intrabaculée. Les sillons sont longs, mais n'atteignent pas en général les pôles. La largueur de l'amincissement autour des sillons est de 1,5 µm. Les endoapertures, de 2 à 3 µm de diamètre, sont de forme circulaire.
Plus grande dimension: 18—26 µm.
Holotype: Planche V, fig. 21, 22, prep. Blao-7; 16,1/105,3.
Derivatio nominis: en hommage à MME. M. VAN CAMPO.
Diagnose différentielle: la forme des endoapertures sépare nettement cette espèce du *G. asiaticus* n. fsp.
Appartenance botanique probable: *Dicotyledonopsida.*

7. *Granotricolporites guinetii* n. fsp. (Planche V, fig. 27—32)

Diagnose

Contour elliptique. Surface granuleuse. L'épaisseur de l'exine est de 1 à 1,8 µm environ, les trois couches de l'ectexine ont la même épaisseur. Structure intrabaculée. Les sillons n'atteignent pas en général les pôles. L'un des sillons est plus court que les deux autres. L'amincissement des sillons est de 1,5 µm de large. Les endopores sont peu visibles, elliptiques de $1 \times 2{,}5$ µm de dimension.
Plus grande dimension: 22—28 µm.
Holotype: Planche V, fig. 27, 28, prep. Blao-11; 5,2/106,4.
Derivatio nominis: en hommage à MONS. PH. GUINET.
Diagnose différentielle: la forme des endoapertures distingue bien *G. guinetii* de *G. vancampoae* n. fsp.
Appartenance botanique probable: *Fagaceae, Cyclobalanopsis* (HUANG 1972).

8. *Granotricolporites* fsp. A (Planche V, fig. 35, 36)

9. *Granotricolporites* fsp. B (Planche V, fig. 37, 38)

Fgen.: *Ilexpollenites* (THIERGART 1937) R. POT. 1960

1. *Ilexpollenites blaoensis* n. fsp. (Planche V, fig. 43—48)

Diagnose

Contour elliptique. La sculpture est 2 µm haute, les clavae ont 1 µm de diamètre environ, mais ce diamètre varie de 0,5 à 2 µm. L'exine est de 2,5—3 µm épaisse. Les

sillons sont longs et atteignent en général les pôles. La largueur des amincissements aux apertures est de 1,5 µm. Les endoapertures sont allongés dans le sens méridien, mesurent de 0,5 à 1×6 à 7 µm.
Plus grande dimension: 20—28 µm.
Holotype: Planche V, fig. 43, 44, prep. Blao-10; 17,7/113,7.
Derivatio nominis: de Blao de la localité type.
Diagnose différentielle: l'exine du *I. auriculoides* ELSIK 1974 est plus épaisse aux pôles (4,5—5 µm) qu'à l'équateur, ce qui distingue bien cette espèce de l'espèce de forme nouvelle.
Appartenance botanique probable: *Ilex*.

Fgen.: *Retitricolporites* (VAN DER HAMMEN 1956) VAN DER HAMMEN et WIJMSTRA 1964

1. *Retitricolporites elongatus* n. fsp. (Planche V, fig. 39, 40)

Diagnose

La forme du pollen est elliptique — allongée, quelquefois fusiforme. Surface réticulée à striée; la maille des réticulations est 0,5 µm ou plus petite. L'épaisseur de l'exine est de 1,5 à 2 µm environ, les trois couches de l'ectexine ont la même épaisseur. Les sillons sont longs, mais n'atteignent pas toujours les pôles. La largueur des amincissements est de 1,5 à 2 µm. Les endopores, de 3—4×8—10 µm de dimensions, sont allongés dans la direction équatoriale.
Plus grande dimension: 30—36 µm.
Holotype: Planche V, fig. 39, 40, prep. Blao-7; 19,3/111,1.
Derivatio nominis: de la forme allongée de l'espèce de forme nouvelle.
Diagnose différentielle: la forme et la réticulation fine séparent nettement cette espèce des autres espèces de ce genre de forme.
Appartenance botanique probable: *Rutaceae, Boenninghausenia* (WANG et al. 1960).

2. *Retitricolporites asiaticus* n. fsp. (Planche V, fig. 41, 42)

Diagnose

Forme allongée. Surface est très finement réticulée à striée. La maille des réticulations et la largueur des murs n'atteignent pas 0,5 µm. L'épaisseur de l'exine est de 1 à 1,5 µm, les trois couches de l'ectexine ont la même épaisseur. Les sillons sont longs, mais n'atteignent pas les pôles, les amincissements sont larges 1,5 µm d'environ. Les endopores sont de forme circulaire de 1,5 à 2 µm de diamètre.
Plus grande dimension: 20—25 µm.
Holotype: Planche V, fig. 41, 42, prep. Blao-18; 19,5/106,3.
Derivatio nominis: de l'Asie.
Diagnose différentielle: la taille et les endoapertures séparent nettement cette espèce de l'espèce de forme nouvelle décrite précédemment.
Appartenance botanique probable: *Dicotyledonopsida*.

3. *Retitricolporites vancampoae* n. fsp. (Planche V, fig. 49, 50)

Diagnose

Pollens elliptiques, quelquefois fusiforme. Les muri sont minces, leur largeur toujours inférieure à 0,5 µm, la maille des réticulations mesure de 1 à 3 µm de dia-

mètre. L'épaisseur de l'exine est de 2 µm, les trois couches de l'ectexine ont la même épaisseur. Les sillons sont longs et atteignent toujours les pôles. Les amincissements sont étroits: 0,5 µm en général. Les endopores sont circulaires, de 2 à 3 µm de diamètre.
Plus grande dimension: 18—24 µm.
Holotype: Planche V, fig. 49, 50, prep. Blao-14; 10,5/111,6.
Derivatio nominis: en hommage à Mme. M. van Campo.
Diagnose différentielle: la maille du réseau plus grande distingue bien l'espèce de *R. asiaticus* n. fsp.
Appartenance botanique probable: *Saxifragaceae, Schizophragma* (Huang, 1972)

4. *Retitricolporites guinetii* n. fsp. (Planche V, fig. 51, 52)

Diagnose

Contour elliptique, quelquefois circulaire. La maille du réseau et les murs mesurent 0,5 µm environ. L'épaisseur de l'exine est de 2 µm environ. Parmi les couches de l'ectexine, la couche infratectale est la plus épaisse. Structure columellaire. Les sillons sont relativement longs, mais n'atteignent pas les pôles. Les amincissements ont 1,5—2 µm de large environ. Les endoapertures sont allongés méridionalement, et mesurent 2×4 µm environ.
Plus grande dimension: 18—25 µm.
Holotype: Planche V, fig. 51, 52, prep. Blao-17; 12,9/117,2.
Derivatio nominis: en hommage à Mons. Ph. Guinet.
Diagnose différentielle: la réticulation plus fine sépare nettement cette espèce du *R. vancampoae* n. fsp. La forme et les amincissements plus larges la distingue *du R. asiaticus* n. fsp.
Appartenance botanique probable: *Dicotyledonopsida.*

5. *Retitricolporites blaoensis* n. fsp. (Planche V, fig. 53—56)

Diagnose

Contour elliptique. La maille du réseau est de 0,5 à 1 µm, les murs sont larges de 0,5 µm environ. Les sillons n'atteignent pas les pôles, l'un parmi ceux-ci est plus court. Il n'y a pas d'amincissements en général. Les endoapertures sont allongés dans la direction de l'équateur de 2—2,5×3—4 µm. L'épaisseur de l'exine de 1 à 1,5 µm, la couche infratectale est la plus épaisse parmi les couches. Structure intrabaculée.
Plus grande dimension: 18—26 µm.
Holotype: Planche V, fig. 53, 54, prep. Blao-15; 11,1/103,1.
Derivatio nominis: de la localité type.
Diagnose différentielle: les sillons, en général sans amincissements séparent nettement l'espèce de *R. asiaticus* n. fsp.
Appartenance botanique probable: *Rutaceae, Clausena* (Wang et al. 1960).

6. *Retitricolporites saurinii* n. fsp. (Planche V, fig. 57, 58)

Diagnose

Pollens elliptique. La maille du réseau est de 1 µm environ, les murs sont de 0,5 µm de large. L'épaisseur de l'exine est de 1,5 à 2 µm; parmi les couches de l'ec-

texine, c'est l'infratectum qui est un peu plus épais que le tectum et la sole. Les sillons n'atteignent pas toujours les pôles, deux sillons sont généralement soudés à leurs extremites. L'amincissement est de 1 à 1,5 µm de large; les endopores sont circulaires, de 2 µm de diamètre.
Plus grande dimension: 25—34 µm.
Holotype: Planche V, fig. 57, 58, prep. Blao-11; 7,1/111,2.
Derivatio nominis: en hommage à MONS. LE PROFESSEUR SAURIN.
Diagnose différentielle: la taille plus grande et les amincissements de l'exine autour des sillons distinguent bien cette espèce de *R. blaoensis* n. fsp.
Appartenance botanique probable: *Leguminosae, Crotolaria* (HUANG 1972).

7. *Retitricolporites rugatus* n. fsp. (Planche V, fig. 59, 60)

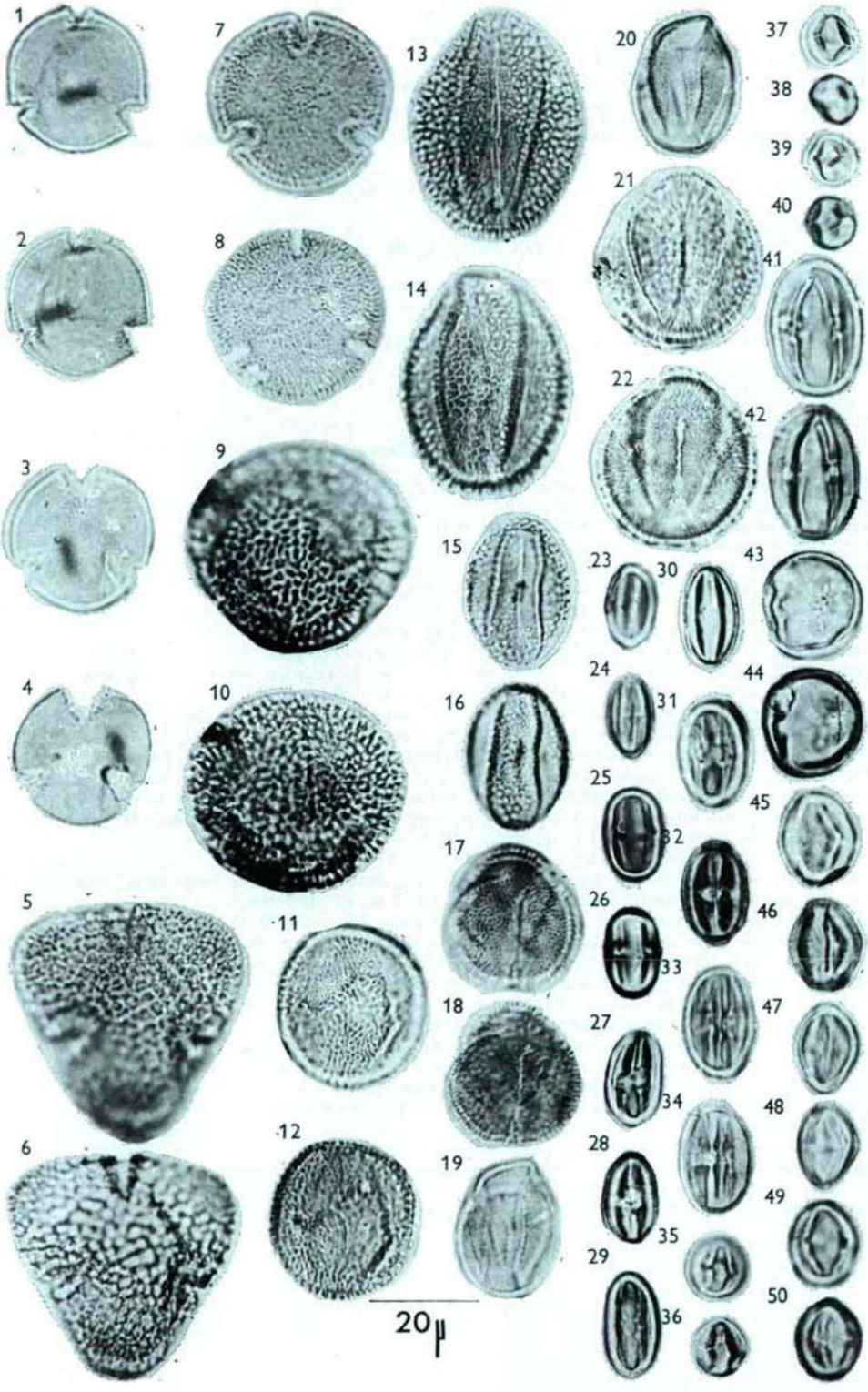
Diagnose

Contour elliptique. La maille des réticulations est de 1 à 1,3 µm, les murs sont large de 0,5 µm. L'épaisseur de l'exine est d'environ 2 µm, les trois couches de l'ectexine ont la même épaisseur. Structure finement intrabaculée. Les sillons n'atteig-

Légende de la Planche IV

Fig. 1, 2. *Tricolpites blaoensis* n. fsp., prep. Blao-8; 8.3/106.3.
Fig. 3, 4. *Tricolpites blaoensis* n. fsp., prep. Blao-2; 8.6/114.4.
Fig. 5, 6. *Bombacacidites vancampoae* n. fsp., *Bombacaceae*, prep. Blao-8; 17.7/110.0.
Fig. 7, 8. *Saurinipollenites circulus* n. fgen. et fsp., prep. Blao-11; 14.3/103.9.
Fig. 9. 10. Forme réticulée, prep. Blao-12; 8.5/112.4.
Fig. 11, 12. Cf. *Retitricolpites* fsp., prep. Blao-5; 11.1/103.6.
Fig. 13, 14. *Retitricolpites guinetii* n. fsp., *Tiliaceae*, prep. Blao-12; 7.3/105.8.
Fig. 15, 16. *Retitricolpites blaoensis* n. fsp., *Hamamelidaceae, Corylopsis*, prep. Blao-4; 14.6/110.3.
Fig. 17, 18. *Retitricolpites vancampoae* n. fsp., cf. *Salicaceae*, prep. Blao-17; 10.2/114.8.
Fig. 19, 20. *Retitricolpites saurinii* n. fsp., *Leguminosae, Smithia*, prep. Blao-19; 12.6/112.5.
Fig. 21, 22. *Retitricolpites crassiexinus* n. fsp., prep. Blao-3; 12.3/111.2.
Fig. 23, 24. *Cupuliferoipollenites oviformis* (R. POT. 1931) R. POT. 1960, *Fagaceae, Castanea*, prep. Blao-18; 17.4/110.8.
Fig. 25, 26. *Cupuliferoipollenites pusillus* (R. POT. 1934) R. POT. 1960, *Fagaceae*, cf. *Castanea*, prep. Blao-12; 8.8/106.1.
Fig. 27, 28. *Cupuliferoipollenites pusillus* (R. POT. 1934) R. POT. 1960, *Fagaceae*, cf. *Castanea*, prep. Blao-13; 18.1/111.3.
Fig. 29, 30. *Cupuliferoipollenites pusillus* (R. POT. 1934) R. POT. 1960, *Fagaceae*, cf. *Castanea*, prep. Blao-16; 18.2/117.0.
Fig. 31, 32. *Fususpollenites fusus* (R. POT. 1931) KDS. 1978, *Fagaceae, Castanopsis* ou *Lithocarpus*, prep. Blao-18; 12.1/115.8.
Fig. 33, 34. *Fususpollenites fusus* (R. POT. 1931) KDS. 1978, *Fagaceae, Castanopsis* ou *Lithocarpus* prep. Blao-18; 18.1/105.7.
Fig. 35, 36. *Cyrillaceaepollenites exactus* (R. POT. 1931) R. POT. 1960, *Cyrillaceae, Clethraceae, Theaceae* ou *Elaeocarpaceae*, prep. Blao-13; 12.9/104.2.
Fig. 37, 38. *Cyrillaceaepollenites exactus* (R. POT. 1931) R. POT. 1960, *Cyrillaceae, Clethraceae, Theaceae* ou *Elaeocarpaceae*, prep. Blao-14; 10.7/103.4.
Fig. 39, 40. *Cyrillaceaepollenites exactus* (R. POT. 1931) R. POT. 1960, *Cyrillaceae, Clethraceae, Theaceae* ou *Elaeocarpaceae*, prep. Blao-1; 19.8/113.8.
Fig. 41, 42. *Psilatricolporites* cf. *laevigatoides* KDS. 1978, cf. *Fabaceae, Campylotropis*, prep. Blao-15; 11.1/103.3.
Fig. 43, 44. *Psilatricolporites asiaticus* n. fsp., prep. Blao-14; 13.1/104.6.
Fig. 45, 46. *Granotricolporites minor* n. fsp., prep. Blao-18; 12.6/110.7.
Fig. 47, 48. *Granotricolporites minor* n. fsp., prep. Blao-19; 18.7/117.0.
Fig. 49, 50. *Granotricolporites minor* n. fsp., prep. Blao-18; 9.4/116.7.

Plate IV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nent pas toujours les pôles, en général l'un est plus court. Des amincissements entourent les endoapertures, leurs largeur est de 2 à 4 µm. Ces endoapertures sont elliptiques et mesurent 3—4×5—6 µm.
Plus grande dimension: 30—40 µm.
Holotype: Planche V, fig. 59, 60, prep. Blao-18; 8,9/109,4.
Derivatio nominis: de la forme des endoapertures.
Diagnose différentielle: la forme des endoapertures distingue bien cette espèce de *R. saurinii* n. fsp.
Appartenance botanique probable: *Dicotyledonopsida.*

8. *Retitricolporites* fsp. A (Planche V, fig. 61, 62)

Appartenance botanique probable: *Rutaceae* (WANG et al. 1960).

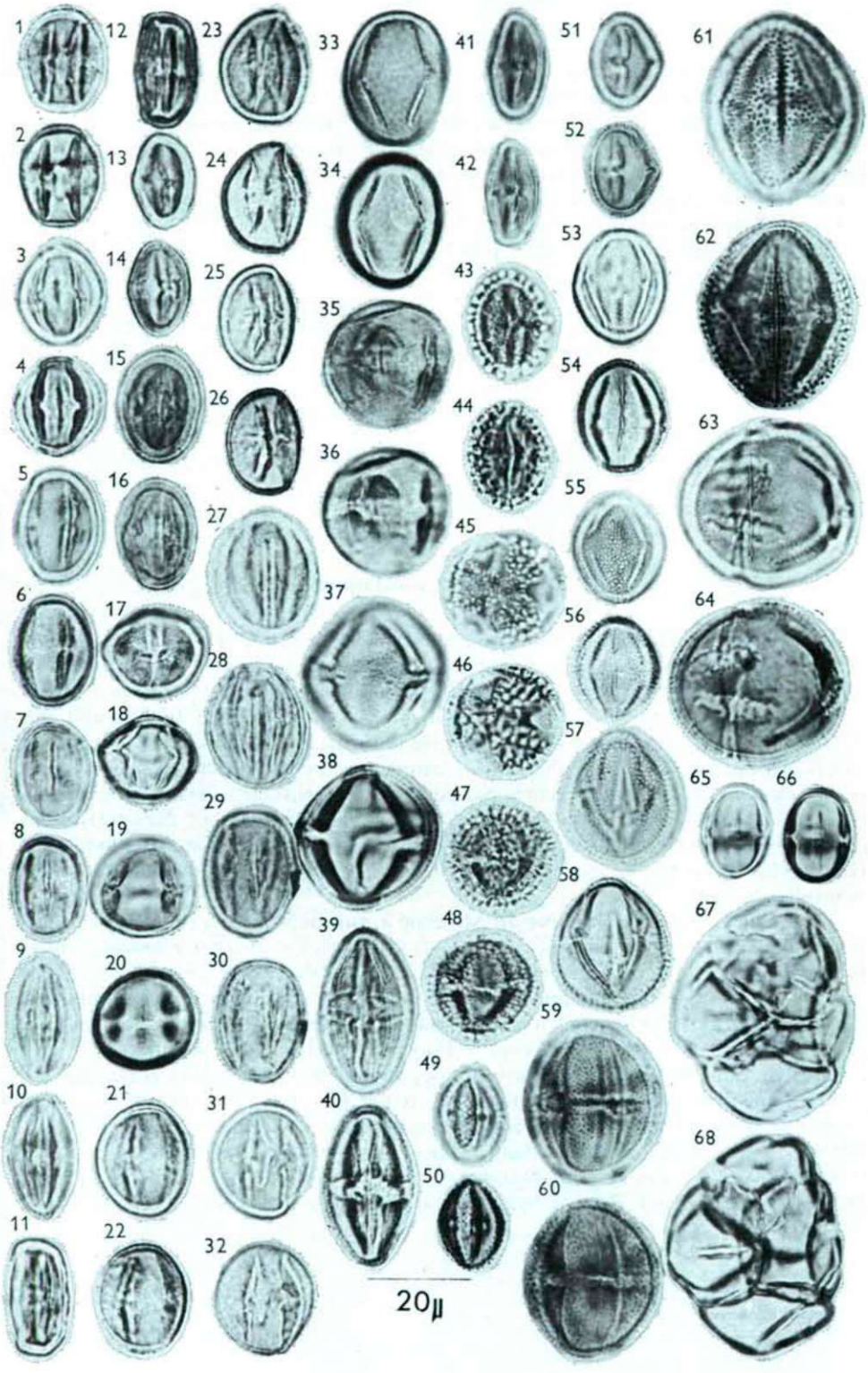
9. *Retitricolporites* fsp. B (Planche V, fig. 63, 64)

Fgen.: *Tetracolporopollenites* PF. et TH. 1953

Légende de la Planche V

Fig. 1, 2. *Granotricolporites asiaticus* n. fsp., prep. Blao-10; 13.8/116.4.
Fig. 3, 4. *Granotricolporites saurinii* n. fsp., prep. Blao-6; 19.0/109.5.
Fig. 5, 6. *Granotricolporites saurinii* n. fsp., prep. Blao-19; 18.1/110.9.
Fig. 7, 8. *Granotricolporites saurinii* n. fsp., prep. Blao-20; 7.8/116.2.
Fig. 9, 10. *Granotricolporites blaoensis* n. fsp., prep. Blao-20; 7.7/113.7.
Fig. 11, 12. *Granotricolporites blaoensis* n. fsp., prep. Blao-18; 14.5/107.3.
Fig. 13, 14. *Intrabaculitricolporites vancampoae* n. fsp., prep. Blao-15; 6.3/117.3.
Fig. 15, 16. *Intrabaculitricolporites guinetii* n. fsp., prep. Blao-18; 6.4/109.8.
Fig. 17, 18. *Granotricolporites circulus* n. fsp., *Rosaceae, Rosa,* prep. Blao-13; 6.4/104.1.
Fig. 19, 20. *Granotricolporites circulus* n. fsp., *Rosaceae, Rosa,* prep. Blao-12; 11.5/114.6.
Fig. 21, 22. *Granotricolporites vancampoae* n. fsp., prep. Blao-7; 16.1/105.3.
Fig. 23, 24. *Granotricolporites vancampoae* n. fsp., prep. Blao-14; 19.1/107.1.
Fig. 25, 26. *Granotricolporites vancampoae* n. fsp., prep. Blao-14; 18.5/116.7.
Fig. 27, 28. *Granotricolporites guinetii* n. fsp., *Fagaceae, Cyclobalanopsis,* prep. Blao-11; 5.2/106.4.
Fig. 29, 30. *Granotricolporites guinetii* n. fsp., *Fagaceae, Cyclobalanopsis,* prep. Blao-20; 6.6/116.8.
Fig. 31, 32. *Granotricolporites guinetii* n. fsp., *Fagaceae, Cyclobalanopsis,* prep. Blao-7; 6.3/106.5.
Fig. 33, 34. *Tetracolporopollenites blaoensis* n. fsp., cf. *Sapotaceae,* prep. Blao-16; 16.8/110.8.
Fig. 35, 36. *Granotricolporites* fsp. A, prep. Blao-18; 16.6/106.3.
Fig. 37, 38. *Granotricolporites* fsp. B, prep. Blao-6; 17.5/114.8.
Fig. 39, 40. *Retitricolporites elongatus* n. fsp., *Rutaceae, Boenninghausennia,* prep. Blao-7; 19.3/111.1.
Fig. 41, 42. *Retitricolporites asiaticus* n. fsp., prep. Blao-18; 19.5/106.3.
Fig. 43, 44. *Ilexpollenites blaoensis* n. fsp., *Aquifoliaceae, Ilex,* prep. Blao-10; 17.7/113.7.
Fig. 45, 46. *Ilexpollenites blaoensis* n. fsp., *Aquifoliaceae, Ilex,* prep. Blao-8; 10.6/111.4.
Fig. 47, 48. *Ilexpollenites blaoensis* n. fsp., *Aquifoliaceae, Ilex,* prep. Blao-12; 19.4/107.9.
Fig. 49, 50. *Retitricolporites vancampoae* n. fsp., *Saxifragaceae, Schizophragma,* prep. Blao-14; 10.5/111.6.
Fig. 51, 52. *Retitricolporites guinetii* n. fsp., prep. Blao-17; 12.9/117.2.
Fig. 53, 54. *Retitricolporites blaoensis* n. fsp., *Rutaceae, Clausena,* prep. Blao-15; 11.1/103.1.
Fig. 55, 56. *Retitricolporites blaoensis* n. fsp., *Rutaceae, Clausena,* prep. Blao-15; 18.2/110.2.
Fig. 57, 58. *Retitricolporites saurinii* n. fsp., *Leguminosae, Crotolaria,* prep. Blao-11; 7.1/111.2.
Fig. 59, 60. *Retitricolporites rugatus* n. fsp., prep. Blao-18; 8.9/109.4.
Fig. 61, 62. *Retitricolporites* fsp. A, prep. Blao-7; 15.6/113.1.
Fig. 63, 64. *Retitricolporites* fsp. B, prep. Blao-11; 12.1/108.7.
Fig. 65, 66. *Tetracolporopollenites halimbaense* KDS. 1961 subfsp. *halimbaense, Sapotaceae,* prep. Blao-9; 9.6/117.2.
Fig. 67, 68. Cf. *Ericipites* fsp., *Ericaceae,* prep. Blao-14; 10,9/111.9.

Plate V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1. *Tetracolporopollenites blaoensis* n. fsp. (Planche V, fig. 33, 34)

Diagnose

Contour elliptique. Sculpture granuleuse, dont les éléments s'anastomosent quelquefois. L'épaisseur de l'exine est de 1 à 1,5 µm environ, les trois couches de l'exine ont la même épaisseur. Structure peu visible au microscope optique. Les sillons s'incurvent vers les pôles et en général se réunissent par paires. L'amincissement est peu marqué, de 0,5 µm environ de large. Les endoapertures sont petites, circulaires, de 1,5 µm de diamètre.
Plus grande dimension: 25—30 µm.
Holotype: Planche V, fig. 33, 34, prep. Blao-16; 16,8/110,8.
Derivatio nominis: de la localité type.
Diagnose différentielle: la forme des sillons sépare bien cette espèce des autres espèces de ce genre de forme, en particulier du *T. sapotoides* Pf. et Th. 1953.
Appartenance botanique probable: cf. *Sapotaceae*.

2. *Tetracolporopollenites halimbaense* Kds. 1961 subfsp. *halimbaense, Sapotaceae* (Planche V, fig. 65, 66)

Fgen.: *Ericipites* Wodeh. 1933

1. Cf. *Ericipites* fsp., *Ericaceae* (Planche V, fig. 67, 68)

Discussion et conclusions

En ce qui concerne les résultats quantitatifs, les pollens des Palmiers *(Feugueuripollenites)* sont dominants, et la quantité des pollens du genre *Ilex* est également remarquable. La quantité de toutes les autres sporomorphes n'atteint pas en général 1%.

Concernant l'âge des sédiments, nous mentionnons les données bibliographiques suivants: Shimada (1955) dans le Pliocène de la formation Yamuke du Groupe Mogami a dénombré 51,8% de pollens d'*Ilex*, auquel viennent s'ajouter les genres *Alnus, Buxus, Juglans* et *Tsuga*. Ces genres par contre manquent dans l'association de type Blao. Pour le Pliocène les pollens fenestrés des *Composées* sont caractéristiques, mais autres types de cette famille se trouvent à partir du Miocène. Mildenhall et Harris (1971) ont mis en évidence des pollens des *Composés* au Pliocène moyen en Nouvelle Zélande.

Dans l'association pollinique du Miocène à Taiwan, Canright (1972) a trouvé des pollens des Angiospermes suivantes: *Liquidambar, Caryapollenites, Alnus, Pinuspollenites, Ilex, Dacrydiumites, Symplocos* et *Polygonum*.

Notre association pollinique ressemble donc assez à celle du Pliocène supérieur du Japon (Shimada 1955) mais n'est pas tout à fait identique. Pour ces raisons l'âge probable parait être Mio—Pliocène, le Pliocène étant le plus probable.

En ce qui concerne la zonation, nous pouvons distinguer deux zones marécageuses, l'une dominée par des palmiers, l'autre par *Ilex*. En se basant sur les travaux récents concernant la végétation actuelle du Sud du Viet-Nam (Barry, Boullet, Phung Trung Ngan et Weiss 1960, Barry, Le Kong Kiet et Vu Van Cu'O'Ng 1961, Barry, Le Cong Kiet et Nguyen Van Thuy 1961, Barry, Le Cong Kiet et Pham Hoang Ho 1961, Barry, Nguyen Van Thuy, Le Cong Kiet et Pham Hoang

Ho (1965) on peut remarquer que la zonation décrite par BARRY, LE CONG KIET et VU VAN CU'O'NG (1961) diffère complétement de notre association reconstitué par les données palynologiques: il semblerait qu'il n'y ait pas de formation équivalente dans la végétation actuelle, à celle du lignite de Blao décrite ici.

En tenant compte que les données palynologiques de cette région de l'Asie sont très limitées et en particulier que pour Viet-Nam c'est la première étude pollinique en dernière analyse nous proposons de prendre cette association comme base, sous le nom de " type Blao ". Des documents plus amples sont nécessaires pour éclaircir les problèmes stratigraphiques et écologiques.

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THE PRESENT DAY STATE OF UPPER CRETACEOUS PALAEOPHYTOGEOGRAPHY ON PALYNOLOGICAL EVIDENCE

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Abstract

Based on published data and original investigations, a new synthesis is presented in this paper for the palynological palaeophytogeography of the Upper Senonian.
Key words: Palynology, Palaeophytogeography, Upper Senonian.

Introduction

The first Senonian palaeophytogeographical provinces for Upper Cretaceous time based on palynological data were published by ZAKLINSKAYA (1962). For the Northern Hemisphere; the *Normapolles, Aquilapollenites, Turkmeno-Kazakhstan, Proteaceae-Olacaceae* and *Proteaceae-Ulmaceae* provinces were distinguished. Later, based on further information, modifications and new data were emphasized in several papers. The aim of this paper is to summarize our present day knowledge in this field.

General problems

A. The problems of palaeophytogeography on the basis of spore-pollen data have been pointed out in several publications. These may be summarized as follows:

1. Stratigraphic problems. — Because of the differences in the composition of the vegetation map and evolution, the palynological time standard is not the same in different parts of the World.
1.1. The same spore or pollen species may have different stratigraphic ranges in different regions.
1.2. Different form-genera or species of different geographical regions may have the same stratigraphic importance.
2. Polar, and continental migrations may be detected on the basis of palynological palaeophytogeography.
3. On the basis of changes in the distribution of spore-pollen genera and types, the most important evolutionary phases (epacme, acme, and paracme) may be established.
4. The factors of evolution may be ascertained by the synthesis of the palaeophytogeography of all geological periods. In this respect, the problem of angiosperm

pollen grains is particularly interesting; DOYLE (1977, 1978), HICKEY and DOYLE (1977), FRIIS and SKARBY (1982), and FRIIS (1983).

B. The methods of the palaeophytogeography differ; but essentially, the presence or absence of spore-pollen groups or genera is important, but the species composition,

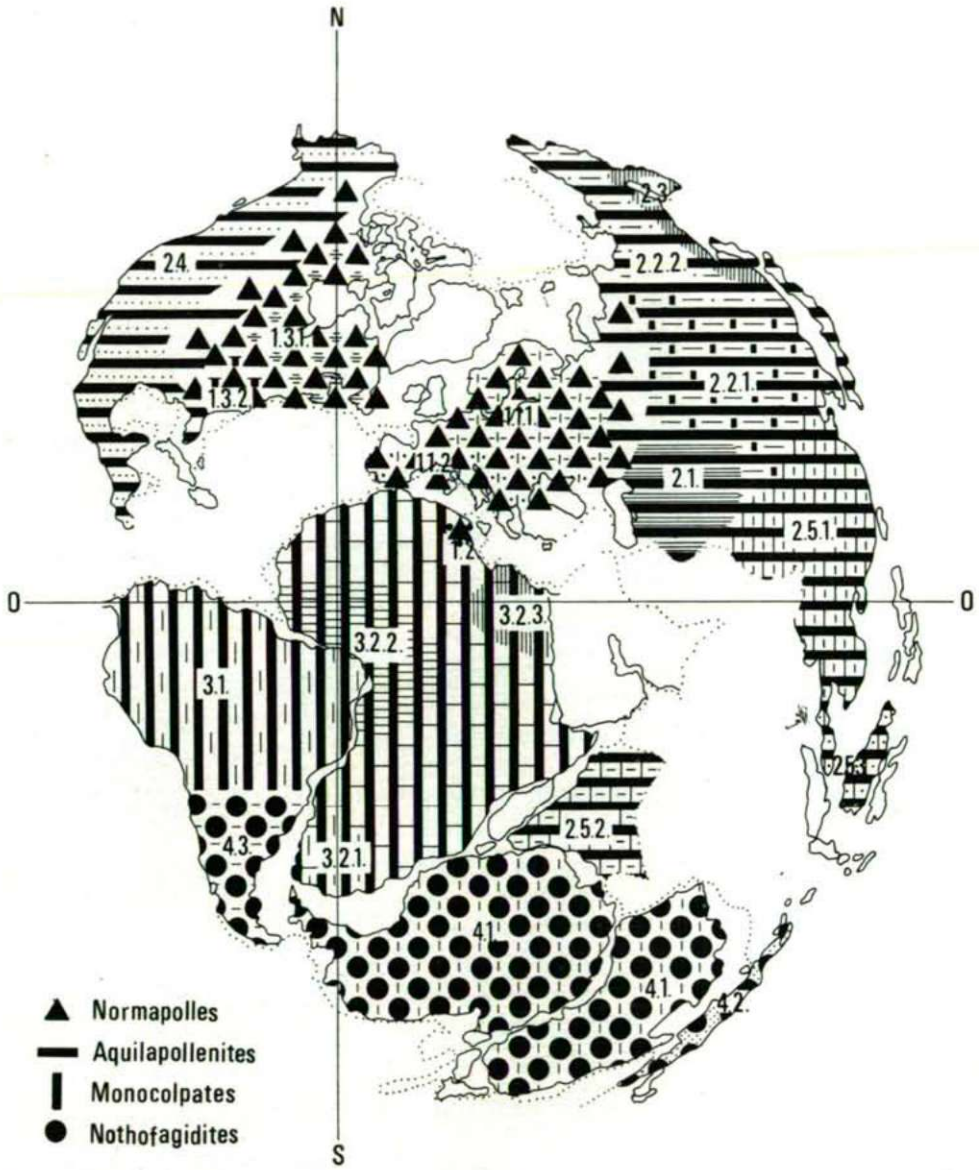

Fig. 1. The present day state of Upper Cretaceous palaeophytogeography on palynological evidence, based on published data and original investigations, compiled by the author in the autumn of 1983.

and the general aspect of the spore-pollen assemblage is also taken into consideration. The effects of the three rules of the fossil spore-pollen assemblages (1. production, 2. dispersion, 3. selective fossilisation) may also differ.

C. The palynological palaeophytogeographical taxa are not yet elaborated. ZAKLINSKAYA (1976) used the kingdom as the highest category. At the present time, however, the province is the most commonly used large palaeophytogeographical unit so that the taxa used are as follows:

province
sub-province
region
sub-region

For our map, we have used fig. 5. of the paper of BRIDEN, DREWRY and SMITH (1974). The decimal system of the text is also indicated on the map, fig. 1.

The Senonian palaeophytogeography of the World based on palynological data

1. province: **Normapolles**

As a palaeophytogeographical unit, this was used first in the paper of KRUTZSCH (1960), but for Lower Tertiary palynomorphs. The most important characteristic feature is the abundance of the early *Amentiflorae* pollen taxa — *Normapolles* —. Geographically this includes the Northern Hemisphere, the Atlantic Coast of North America and Tunisia. Pollen of this group may occur in other regions too, but these occurrences are not of the first rank from the palaeophytogeographical point of view.

1962, ZAKLINSKAYA—*Normapolles* Province
1967, KRUTZSCH—*Normapolles* Provincia
1970, MULLER — North Atlantic—European Province
1971, KHLONOVA — European—Turanian Province
1978, GRUAS—CAVAGNETTO — European—N. Atlantic Province
1978, SRIVASTAVA—*Normapolles* Province
1980, HERNGREEN — The Upper Cretaceous *Normapolles* Province
1981, HERNGREEN and CHLONOVA — *Normapolles* Province

From the literature, we refer the following opinions:

GRUAS-CAVAGNETTO (1978), p. 7: "La flore américaine aurait évolué plus rapidement que la flore européenne, si l'on en juge par le remplacement des pollens de *Normapolles* par des pollens de taxons actuels qui s'est effectué plus lentement en Europe qu'en Amérique du Nord." TSCHUDY (1980) published a World map of the end of the Cretaceous modified from DIETZ and HOLDEN (1971) and TEDFORD (1974). Later TSCHUDY (1981) discussed the geographic distribution of *Normapolles* genera in North America and established the following; p. 283: "At least six genera having *Normapolles* characteristics occur in eastern North America but have not yet been recorded from Europe. Two additional genera with *Normapolles* characteristics have been reported only from the *Aquilapollenites* province of western North America.", p. 310: "The first *Normapolles* genera to migrate to North America did so in Cenomanian time, probably via the still-open North Atlantic corridor. Limited

secondary migrations from eastern North America to the Western Interior took place across the midcontinental epeiric seaway during the Late Cretaceous, and further migrations continued after the withdrawal of the sea up until the final extinction of this group in late Eocene time." Taking into consideration the details, several parts may be distinguished inside the *Normapolles* province. KRUTZSCH (1967, in GÓCZÁN et al.) distinguished the Mediterranean part of the *Normapolles* province in Europe, and he added to this the northern part of North Africa (North Morocco, Algeria and Tunisia). MÉDUS (1973) followed this distinction with nomenclatural modification and introduced the Mesogean region (=Mediterranean) of the *Normapolles* province. The northern part is the Boreal region. Based on data from Senonian palynomorphs of Portugal together with other palynomorphs from the Mesogean region, KEDVES and DINIZ (1983) published the following:

1.1. sub-province: **European**

This sub-province may be characterized by the greatest number of *Normapolles* genera, most of them occurring only within this territory.

1.1.1. region: *Boreal*

The most abundant genera: *Trudopollis, Pseudoplicapollis, Plicapollis, Minorpollis, Pseudovacuopollis, Interporopollenites, Pseudoculopollis, Vacuopollis, Bohemiapollis, Oculopollis, Semioculopollis, Pecakipollis, Papillopollis, Pseudotrudopollis, Extratriporopollenites, Magnoporopollis.*

1.1.2. region: *Mesogean (=Mediterranean)*

MÉDUS (1973) pointed out the following as Mesogean genera: *Bakonyipollis, Capipollis, Endopollis, Hungaropollis, Laudaypollis, Primipollis, Pseudopapillopollis Schulzipollis, Szoerenyipollis.*

1.1.2.1. sub-region: *Ibero-lusitanian*

Abundant genara: *Interporopollenites, Vacuopollis, Papillopollis.* By their presence important genera: *Vancampopollenites, Triangulipollis, Trevisanaepollenites, Prenudopollis, Mediterraneipollenites, Boltenhagenipollenites, Magnoporopollis, Aveiropollenites.*

1.1.2.2. sub-region: *Pyrenean*

The following are worth mentioning: *Interporopollenites, Suemegipollis, Oculopollis, Papillopollis, Heidelbergipollis, Magnoporopollis, Longanulipollis, Trudopollis, Emscheripollis, Krutzschipollis, Pompeckjoidaepollenites.*

1.1.2.3. sub-region: *Carpathian*

Characteristic genera: *Complexiopollis, Oculopollis, Laudaypollis, Hungaropollis, Longanulipollis, Suemegipollis, Krutzschipollis, Verruoculopollis, Portaepollenites, Semioculopollis, Papillopollis, Interporopollenites.*

1.2. sub-province: **Tunisian**

MEON and DONZE (1983) investigated the Upper Maestrichtian — Danian sporepollen assemblages of Kef (N. W. Tunisia). The following *Normapolles* genera were shown from this material: Cf. *Elsikipollenites, Hofkeripollenites, Lusatipollis, Magnoporopollis, Minorpollis, Nudopollis, Oculopollis, Plicapollis, Pseudoculopollis, Semioculopollis, Stephanoporopollenites, Trudopollis.* In this way, the Upper Cretaceous flora of Tunisia seems to be completely different from those in Egypt or other parts of North Africa.

1.3. sub-province: **Atlantic Coast of North America**

As was pointed out in several papers the number of *Normapolles* genera is less than in Europe, but on the other hand there are characteristic North American types too. TSCHUDY (1975) pointed out the following; p. 1: "At the present time, 57 *Normapolles* genera have been reported from Europe, 47 from boreal Middle Europe and 10 from western Hungary. Only four *Normapolles* genera are common to the two European regions. In Mississippi embayment rocks I have found pollen assignable to 18 of the European *Normapolles* genera, to 2 additional genera previously described from the United States, and to 4 new genera that I have proposed."

1.3.1. region: *North Atlantic Coastal Plain*

TSCHUDY (1981) published the following form-genera: *Atlantopollis, Basopollis, Bohemiapollis, Complexiopollis, Choanopollenites Emscheripollis, Endoinfundibulapollis, Extremipollis, Heidelbergipollis, Interpollis, Kyandopollenites, Longanulipollis, Megatriopollis, Minorpollis, Nudopollis, Osculapollis, Pecakipollis, Piolencipollis, Plicapollis, Pompeckjoidaepollenites, Praebasopollis, Praecursipollis, Primipollis, Pseudatlantopollis, Pseudosculapollis, Pseudoplicapollis, Pseudovacuopollis, Quedlinburgipollis, Semioculopollis, Thomsonipollis, Trudopollis, Vacuopollis.*

1.3.2. region: *Mississippi embayment*

Form-genera list after TSCHUDY (1981): *Atlantopollis, Basopollis, Complexiopollis Choanopollenites, Endoinfundibulapollis, Extremipollis, Interpollis, Kyandopollenites, Megatriopollis, Minorpollis, Nudopollis, Osculapollis, Pecakipollis, Plicapollis, Pompeckjoidaepollenites, Praecursipollis, Pseudatlantopollis, Pseudoculopollis, Pseudoplicapollis, Pseudovacuopollis, Semioculopollis, Thomsonipollis, Trudopollis, Vacuopollis, Interporopollenites.*

2. province: **Aquilapollenites**

The most important characteristic feature is the presence of *Triprojectacites* (see STANLEY, 1970) and other genera for example *Wodehouseia, Orbiculapollis* etc. Geographically, Northern Hemisphere, Siberia, Far East, the Pacific Region of North America, the southern part of Asia, including China and India. *Aquilapollenites* occurs in the British Isles, and in Equatorial Africa also. It seems that the first evolution centre was in Siberia, but this was not the only centre of occurrence. Another important centre is the Equatorial African one. The European (British Isles) occurrence is an interesting and curius local one.

1962, ZAKLINSKAYA — *Aquilapollenites* Province
1967, KRUTZSCH — Siberian—Pacific Province
1970, MULLER—E. Siberian—N. Pacific Province
1971, KHLONOVA — Siberian—Pacific Province; Siberian—Canadian Province
1978, GRUAS—CAVAGNETTO — Pacific—Siberian Province
1978, SRIVASTAVA — *Aquilapollenites* Province
1980, HERNGREEN — The Upper Cretaceous *Aquilapollenites* Province
1981, HERNGREEN and CHLONOVA — *Aquilapollenites* Province

KEDVES and KIRÁLY (1970) discussed the regional distribution of the different types of *Triprojectacites (Aquilapollenites)* and *Wodehouseia, Azonia, Jacutiana, Orbiculapollis* and *Expressipollis*. The southern borders of these pollen in Siberia are further south than in North America.

2.1. sub-province: **Turkmeno-Kazakhstan**

1962, ZAKLINSKAYA — Turkmeno-Kazakhstan Province
1971, KHLONOVA — Turkmeno-Kazakhstan Province
1978, GRUAS—CAVAGNETTO — Turkmeno-Kazakhstan Sub-province

There is a peculiar mixed flora here. Based on the publication of POLUMISKOVA et al. (1966), the following form-genera are worth mentioning: *Mancicorpus, Aquilapollenites, Wodehouseia, Proteacidites, Trudopollis, Plicapollis, Oculopollis.* The genus *Betpakdalina* (ZAKLINSKAYA, 1966) is a characteristic feature of this sub-province.

2.2. sub-province: **Siberian**

Characteristic are the *Triprojectacites,* with *Wodehouseia, Azonia* etc. SAMOILOVICH (1967) published the following distinction: 1. Yenisey—Amur, and 2. Khatanga—Lena provinces. These are considered as regions according to our system. They display the following palynological characteristics based on the publication of SAMOILOVICH (1967).

2.2.1. region: *Yenisey—Amur*

Palmae gen. sp., *Beaupreaidites, Proteacidites* fspp., *Loranthacidites, Elythranthe, Aquilapollenites* fspp., *Mancicorpus, Parviprojectus, Expressipollis, Orbiculapollis, Wodehouseia.*

2.2.1.1. sub-region: *Ust—Yenisey*

Anacolosidites grandis, Duplosporis ocliferus, D. borealis, Pemphixipollenites fspp. *Integricorpus.* BONDARENKO (1973) published the following important taxa: *Aquilapollenites* fspp., *Anacolosidites grandis, Mancicorpus, Pemphixipollenites* fspp., *Ulmoideipites, Expressipollis, Orbiculapollis, Parviprojectus, Myrica, Almus, Ulmaceae, Pterocarya, Loranthacites, Azonia reticulata, Wodehouseia calvata, Beaupreaidites, Triprojectus, Syncolpites, Proteacidites, Trudopollis, Nudopollis.*

2.2.1.2. sub-region: *Middle Yenisey*

Proteacidites fspp., *Symplocacites sibiricus, Aquilapollenites* fspp., *Projectoporites* fspp.

2.2.1.3. sub-region: *Baikal—Zeya—Bureya*

Ulmoideipites fspp., *Symphyonema, Santalumidites, Haloragacidites,* cf. *Nyssa, Tricolpites mataurensis.*

2.2.2. region: *Khatanga—Lena*

Myrica, Comptonia spp., *Juglans, Pterocarya, Quercites, Menispermum, Symplocacites, Tetraporites, Gothanipollis* fspp., *Duplodemicolpate, Retitricolpites* fspp., *Integricorpus* fspp., *Aquilapollenites* fspp., *Parviprojectus* fspp., *Mancicorpus, Wodehouseia* fspp., *Azonia* fspp., *Jacutiana.*

2.3. sub-province: **Primorsko-Sakhalin**

1969, BRATZEVA — Primorsko—Sakhalin Sub-province
1977, ZAKLINSKAYA — Primorsko—Sakhalin Province
1978, GRUAS—CAVAGNETTO — Primorsko—Sakhalin sous-province
1982, KREMP — Primorsk—Sachalin Province

ZAKLINSKAYA (1977) described the following form-genera from the Senonian sediments of Sakhalin: *Aquilapollenites, Integricorpus, Scollardia, Cranwellia, Orbiculapollis.* Japan is very important within this sub-province. New data have been provided by the monographical work of TAKAHASHI and SHIMONO (1982). They

published a typical *Aquilapollenites* type assemblage from the Maestrichtian layers of the Miyadani-gawa Formation, Hida district, Central Japan. As important genera, we enumerate the following: *Cranwellia, Orbiculapollis, Wodehouseia, Aquilapollenites, Hemicorpus, Pseudointegricorpus, Triprojectus, Fibulapollis, Mancicorpus.*

2.4. sub-province: **Pacific Coast of North America**

TSCHUDY (1980) emphasized the following; p. 5: "In North America during the Cretaceous, these two provinces were separated by a great north-south-trending epeiric sea..." "Fossil pollen from the western segment of North America during latest Cretaceous time is characterized by pollen of many species of the genus *Aquilapollenites* and by several other genera, such as *Cranwellia, Scollardia* and *Wodehouseia, ...*"

(2.4.1.) region: *Southern Rocky Mountains*
(2.4.2.) region: *Northern Rocky Mountains*
(2.4.3.) region: *Western Canada*
(2.4.4.) region: *California.*

The most important characteristic palynological features of these regions are not yet elaborated and because of this, they are not represented on our figure.

2.5. sub-province: **South Asiatic**

The presence of the *Aquilapollenites* is important here, but there is a lack of *Wodehouseia* and other forms of the "oculata" type.

2.5.1. region: *South East Asiatic*

We refer to the data of the following papers: SUNG TZE-CHEN and LEE MANY-ING (1976), WANG DA-NING and ZHAO YING-NIANG (1979), SONG ZHI-CHEN (1980), SONG ZHICHEN et al. (1980). The following are worth mentioning: *Aquilapollenites, Parviprojectus, Translucentipollis, Cranwellia, Morinoipollis, Jianghanpollis, Jiangsupollis, Myoporumpollenites, Lythraites, Crassimarginipollenites, Bozhengpollis.* Based on the paper of SONG ZHI-CHEN (1980), two sub-regions may be distinguished in the Upper Cretaceous vegetation of China.

2.5.1.1. sub-region: *Northeast China*

SONG ZHI-CHEN (1980), p. 2: "The palynological assemblages of the Northeastern China Region are characterized by 1) a greater number of *Cyatheaceae* and *Polypodiaceae*, and less a number of *Schizaeoisporites* in spores; 2) the more abundant pollen grains of saccated elements in conifer than those of *Classopollis*, 3) the *Aquilapollenites* developing more than those of the Central China Region and 4) the absence of *Bozhengpollis* and *Jiangsupollis*."

2.5.1.2. sub-region: *Central China*

SONG ZHI-CHEN (1980), p. 2: "The palynological assemblages of the floristic regions of Central China are dominated by *Schizaeoisporites, Pterisisporites* and *Classopollis*. The *Aquilapolles* are rather less than those of the former region, and the species of *Bozhengpollis* and *Jiangsupollis striatus*, etc. are more or less recorded, ..."

2.5.2. region: *Indian*

The Indian peninsular province was described first by SRIVASTAVA (1978). GRUAS—CAVAGNETTO (1978) pointed out the following; p. 7: "Dans les régions orientales, les palynoflores sont assez semblables à celles de Bornéo au Crétacé supérieur et au Paléocène, ..." "Dans le Sud de l'Inde, on rencontre des rélictes gondwaniens au Crétacé supérieur et la palynoflore est semblable à celle d'Australie. A re-

marquer la présence, dans cette région d'*Aquilapollenites*, élément typique de la province sibérienne." The following genera are important: *Aquilapollenites, Cranwellia, Scollardia, Pulcheripollenites* and *Proxapertites*. Gondwana elements: *Andreisporis, Constantinisporis, Victorisporis*.

2.5.3. region: *Malaysian*

1978, GRUAS—CAVAGNETTO — Malaise province

MULLER (1968) described Upper Cretaceous spore-pollen assemblages from Borneo. The following form-genera are important: *Spinizonocolpites, Proxapertites, Dicolpopollis, Triorites, Verrutriporites, Echitriporites, Aquilapollenites, Rugutriporites, Retitriporites*. Later MULLER (1970) emphasized the following; p. 433: "It is significant that in Borneo no proteaceous pollen types occur..."

3. province: **Monocolpates**

1967, KRUTZSCH — African—?South American Province
1978, GRUAS—CAVAGNETTO — Africano—Sud-American Province
1978, SRIVASTAVA — *Galeacornea—Constantinisporis* Province
1980, HERNGREEN — The Late Cretaceous *Palmae* Province of Africa and Northern South America
1981, HERNGREEN and CHLONOVA — *Palmae* Province

The most important elements are *Cycadopites, Monocolpopollenites, Retimonocolpites* and *Liliacidites*. Geographically Africa, except Tunisia, and the northern part of South America belong to this province. Some selected remarks: MULLER (1970); p. 432: "There are indications that the W. African and N. South American microfloras of this period were rather similar. For instance the form-genus *Buttinia* is characteristic for this period in both areas." JARDINÉ et al. (1974); p. 81: "—à ce moment apparaissent des pollens triporés ornés caractéristiques du type *Echitriporites* ou *Proteacidites* dans presque tous les bassins africains et américains, y compris la Colombie et la Venezuela (GERMERAAD et al., 1968). — des espèces comme *Auriculiidites articulatus* au Santonien-Maestrichtien; *Buttinia andreevi* et *Spinizonocolpites baculatus* au Maestrichtien soulignent également une communauté pan-afro—sud-américaine jusqu'à la fin du Crétacé." GRUAS—CAVAGNETTO (1978), p. 7: "La province 'Africano—Sud-Américaine' englobe l'Ouest africain et le Nord de l'Amérique du Sud. Le genre *Buttinia* caractérise cette province." SRIVASTAVA (1978, 1981) distinguished the *Constantinisporis* province for the northern part of South America and for the middle and/or northern part of Africa.

3.1. sub-province: **Northern part of South America**

As was previously emphasized, there are similarities between the microflora of northern South America and Africa. It is necessary, however, to pointed out the differences too. *Aquilapollenites* sensu stricto is absent in South America, and *Crassitricolpites, Crassitriaperturites* and *Psilastephanocolporites* are the characteristic elements here.

3.2. sub-province: **African**

The Senonian flora of Africa is more complex than was previously belived. For example, the Senonian flora of North Africa (excluding Tunisia) is also different. The monocolpate group may be characteristic with other elements, which have further regional value.

3.2.1. region: *South African*

The first publication of Upper Cretaceous palynomorphs was that of KIRCHHEIMER (1932) from "Arbot" Pipe on the Bushmanland Plateau in Namaqualand. In this assemblage, the pollen of *Myrica* was dominant, but bisaccate gymnosperm and proteaceous types also occurred. Based on a letter from DR. J. A. COETZEE (Bloemfontein, Orange Free State), the geological age of these layers may be younger than Senonian, however new research is in progress (SCHOLTZ, 1984). Thus the age of this region is in question, but it must be emphasized that up until this time, the form-genus *Nothofagidites* has not been published from this region. In spite of this, SRIVASTAVA (1981) included South Africa in the *Nothofagidites* province.

3.2.2. region: *West-Equatorial African*

Including: Gabon, Cameroon, Nigeria, Ivory Coast, Senegal and the Mali-Niger syncline. This is the most elaborated region. The most important elements are the following: *Buttinia, Pediculisporis, Aquilapollenites, Translucentipollis, Andreisporis,* and *Constatinisporis.*

3.2.3. region: *Egyptian*

The regional distribution of this spore-pollen assemblage type is not well known at the moment. Sudan and Libya may belong here in part. Arabia is also a problematical area. The most important elements include: **Saadipollenites, *Dettmannaepollenites, *Souwonmiaepollenites, Beaupreaidites, Annutriporites, *Minquaripollenites.* The from-genera designated with an asterisk will appear in a monographical study of the Upper Cretaceous spore-pollen assemblages of Egypt which is currently in preparation.

4. province: **Nothofagidites**

1978, SRIVASTAVA — *Proteacidites—Nothofagidites* Province
1980, HERNGREEN — The Senonian *Nothofagidites* Microfloral Province
1981, HERNGREEN and CHLONOVA — *Nothofagidites* Province.

The most important characteristic features here are *Nothofagidites* and *Proteaceae* pollen grains. Geographically: Australia, New Zealand, Antarctica, and the southern part of South America.

The following remarks seems to be importants: MULLER (1970), p. 433: "In the south, the Australian—Antarctic province can be distinguished, with dominance of *Nothofagus* and proteaceous pollen types." The Quiriquina Formation (Upper Cretaceous, Senonian) according to DOUBINGER (1972) is similar to tropical South America (Colombia, Venezuela) and to Occidental Africa (Senegal, Gabon). GRUAS—CAVAGNETTO (1978), p. 7: "Dans la province 'Antarctico—Australienne' dominent les pollens de *Nothofagus* et de Protéacées." HERNGREEN (1980), p. 82: "The late Cretaceous assemblages from Australia, New Zealand, Antarctica and Fuegia/Patagonia are characterized by the occurrence of *Nothofagidites.* Other diagnostic forms are *Proteacidites* spp., and trisaccate gymnosperms." MILDENHALL (1980), p. 197: "A similar vegetational history of *Nothofagus* in Australia, New Zealand and South America can only be explained if the gene pool was similar in each area; this implies continual contact." SRIVASTAVA (1981) added South Africa too to this province.

4.1. sub-province: **Antarctio-Australian**

1970, MULLER — Australian—Antarctic Province
1976, ZAKLINSKAYA — Australian—Antarctic Province.

We have palynological data principally from Australia; the following form-genera are important: *Microcachrydites, Phyllocladidites, Proteacidites, Propylipollis, Nothofagidites*. From Antarctica, there is less information, see for example the paper of WILSON (1968).

4.2. sub-province: **New Zealandian**

ZAKLINSKAYA (1977) distinguished this palaeophytogeographical unit. Based on the monographical work of COUPER (1960), the following form-genera are worth mentioning: *Liliacidites, Beaupreaidites, Proteacidites, Triorites, Nothofagidites.*

4.3. sub-province: **Patagonian**

Geographically, the southern part of South America, with *Nothofagidites*. As regards the world-wide distribution of this above mentioned form-genus, see the paper of CRANWELL (1964). For this sub-province, further information comes from ARCHANGELSKY and ROMERO (1974).

Discussion and conclusions

The LAMBERT equal-area projection method, used for Cretaceous time by BRIDEN et al. (1974) is very useful for the solution and proposal of questions. Based on our new data the following may be pointed out:

1. From a palaeophytogeographical point of view, in Senonian time, Madagascar is most important, because it is situated near three provinces *(Aquilapollenites, Nothofagidites* and *Monocolpates)*. Therefore, a peculiar mixed pollen flora may be presumed here.
2. Further interesting areas, for palynological investigations:

2.1. Southern part of Arabia; question: is the genus *Aquilapollenites* present here together with the so-called Gondwana elements?

2.2. Iraq and Iran; the presence of *Normapolles* and *Aquilapollenites* is in question here.

2.3. Guinea and Sumatra have peculiar importance for the *Aquilapollenites* — *Nothofagidites* province border.

2.4. The western part of North Africa, principally Morocco, may also belong to the *Normapolles* province, together with Tunisia.

3. The southern border of the *Normapolles* and *Aquilapollenites* province is asymetric; in Eurasia it is more southerly than in North America (cf. KEDVES and KIRÁLY, 1970). The LAMBERT equal-area projection method demonstrates this well.
4. In the northern and the southern hemispheres a "biological asymetry" may also be established, based on the following:

4.1. The *Nothofagidites* pollen type is identical with recent *Nothofagus* pollen. The Upper Cretaceous distribution is approximately the same as at present. The problem of the *Monocolpates (Cycadales, Palmae)* pollen type is similar.

4.2. The *Normapolles,* and the *Aquilapollenites (Triprojectacites)* group are extinct pollen types, without well established botanical affinities, so there are no recent distributions.

This is the essence of this "biological asymetry". Finally there are a number of problems to solve, I hope, that the present contribution will be useful for further research.

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LM, TEM AND SEM INVESTIGATIONS ON RECENT INAPERTURATE GYMNOSPERMATOPHYTA POLLEN GRAINS

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Abstract

LM investigations on recent *Taxodiaceae* and *Cupressaceae* pollen grains refer to that the "hiatus" form depend not only on the conditions of the preservation, but in certain cases, the dubius/hiatus proportion have taxonomical value. From the new TEM data on the exine of *Sequoia sempervirens*, it may be emphasize, that the most outer layer of the ectexine may detached easily. The main conclusion of the SEM data is that conclusions of taxonomic value can only be concluded from the totality of the data. In this way, by the joint evaluation of the surface of the orbiculi, the papilla, the proximal, and the distal pole can be got differential data.
Key words: Palynology, recent, *Taxodiaceae*, *Cupressaceae*, LM, TEM, SEM.

Introduction

The importance of the inaperturate pollen grains in the Tertiary sediments of the Northern Hemisphere was emphasized by the early palynological researches. POTONIÉ (1931, 1934) in his paper of 1934 as recent comparative material used the pollen grains of the following species: *Sequoia sempervirens, Taxodium distichum, Larix europea, Juniperus communis, Cupressus sempervirens, C. benthani, Libocedrus decurrens*. WODEHOUSE (1933) from the oil shale of the Green River Formation described the *Taxodium hiatipites, Glyptostrobus vacuipites* and *Cunninghamia concedipites* and as botanical affinity the *Cupressineae, Taxodineae* and *Taxineae* were established. E. NAGY (1958) discussed in detail the problems of the taxonomy and nomenclature of the fossil inaperturate pollen grains. TEICHMÜLLER (1958) pointed out the importance of the *Taxodiaceae* pollen grains in the zonation of the vegetation of the Tertiary brown coal formation.

In connection with the light microscope studies of the recent taxa, the following works are worth mentioning: M. VAN CAMPO in her work of 1951 dealt with the genuses of the *Taxodiaceae* family; *Sciadopitys, Cunninghamia, Sequoia, Wellingtonia, Glyptostrobus, Crytomeria, Taiwania, Athrotaxis, Metasequoia, Taxodium*. Later (M. VAN CAMPO-DUPLAN, 1953) the genuses of the *Cupressaceae* family were the subject of her work *(Biota, Thujopsis, Heyderia, Cupressus, Chamaecyparis, Thuja, Fokiena, Juniperus, Actinostrobus, Fitzroya, Tetraclinis, Diselma, Libocedrus, Widdringtonia, Callitris)*. The first transmission electronmicroscopical results were published by AFZELIUS (1956); *Larix decidua, Cephalotaxus nana*, further data in the publication of UENO (1959, 1960a, b) and GULLVAG (1966). The carbon replica method for these pollen grains was employed by ERDTMAN (1965); *Cryptomeria, Meta-*

sequoia, Thuja, Thujopsis, Cephalotaxus, Chamaecyparis, Juniperus. The first scanning electronmicroscopical results were published by REYRE (1968), this work is fundamental from several point of view, and because of the elaboration of numerous taxa: *Araucaria, Taiwania, Cryptomeria, Sequoiadendron, Taxodium, Cupressus, Juniperus, Widdringtonia, Callitris, Libocedrus, Cephalotaxus, Taxus, Torreya.* In this respect the monographical work of PLANDEROVÁ is worth mentioning (1976). TEM data about fossil inaperturate pollen grains are rather scarce (KEDVES and PÁRDUTZ, 1973, 1974). First SEM results from fossil inaperturate pollen grains were published by REYRE (1968), further rich documentation can be found in the monographical work of REYRE (1973).

During my LM, TEM and SEM investigations on recent *Taxodiaceae, Cupressaceae* and *Taxaceae* pollen grains, the LM, TEM and SEM methods were applied. The aim of this paper is the following:

1. The establishment of the taxonomic value of the morphologic types, used at the fossil forms.
2. The TEM data are complementary to the earlier publications, but they may serve informations to the SEM data.
3. The SEM data have generally taxonomic value. In this paper the possibility of the submicroscopic ornamental elements in the establishment of the botanical affinities was the subject of the present investigations.

Material and methods

LM studies were made on the slides mounted in the Palynological Laboratory, Stockholm—Solna for the sake having of constant preparation method. I wish to express my acknowledgments to DR. S. NILSSON for his kind assistance. The species investigated are as follows: *Sequoia sempervirens* (LANB.) ENDL., *Taxodium mucronatum* TENORE, *Cryptomeria japonica* (L. F.) DON., *Cupressus arizonica* GREENE, *Cupressus funebris* ENDL., *Cupressus macrocarpa* HARTW. var. *guadalupensis* MASTERS, *Cupressus lusitanica* MILL., *Cupressus sempervirens* L., *Chamaecyparis thyoides* (L.) SARGENT, *Chamaecyparis nootkatensis* (LANB.) SPACH, *Chamaecyparis obtusa* ENDLICHER, *Chamaecyparis lawsoniana* (MURR.) PARL., *Chamaecyparis pisifera* SIEB. et ZUCC., *Juniperus chinensis* L.' *Thuja plicata* DON., *Taxus cuspidata* SIEB. et ZUCC., *Cephalotaxus harringtoniana* K. KOCH var. *drupaceae* KOIDZ. For electronmicroscopical investigations numerous botanical gardens helped me kindly with pollen material. *Sequoia sempervirens* (LANB.) ENDL. (Hortus Botanicus, Coimbra, Portugal) was investigated by the TEM method. OsO_4 aq. dil. was used for fixing, the pictures were taken on Tesla BS-500 electron microscope in the EM Laboratory of the Faculty of the J. A. University, Szeged. For his kind assistance I am deeply indepted to DR. I. ROJIK. The submicroscopic ornamentation was studied by the scanning electron-microscope of the following species: *Sequoia sempervirens* (LANB). ENDL. (Hortus Botanicus, Coimbra, Portugal), *Sequoia gigantea* TORR. (Botanischer Garten der Universität, Freiburg, B. R. D.), *Taxodium distichum* RICH. (Istituto e Orto Botanico, Roma, Italy), *Taxodium mucronatum* TENORE (Istituto e Orto Botanico, Roma, Italy), *Cryptomeria japonica* (L. F.) DON., (Istituto e Orto Botanico, Roma, Italy), *Cupressus arizonica* GREENE (Hortus Botanicus, Coimbra, Portugal), *Cupressus funebris* ENDL. (Hortus Botanicus, Coimbra, Portugal), *Cupressus macrocarpa* HARTW. var. *macrocarpa* (Hortus Botanicus, Coimbra, Portugal), *Callitris cupressiformis* VENT. (Hortus Botanicus, Coimbra, Portugal). The air-dryed pollen grains were mounted on polyvinilchlorid adhesive, and were coated with gold-palladium. The pictures were taken in the Electronmicroscope Laboratory of the Zoological Department of the E. L. University on a JSM-50A scanning electron microscope. I express my thanks to DR. J. KOVÁCS lecturer for his kind help.

Results and discussion

A) THE PER CENTS OF THE MORPHOLOGICAL TYPES of the studied species are summarized in the following table. Under names of the species, the number of the specimens investigated may be shown.

	dubius form without papilla	dubius form with papilla	hiatus form without papilla	hiatus form with papilla
Sequoia sempervirens 209	35.9	38.2	20.1	5.7
Taxodium mucronatum 202	44.6	54.9	0.5	0.0
Cryptomeria japonica 210	0.0	100.0	0.0	0.0
Cupressus arizonica 195	92.3	7.7	0.0	0.0
Cupressus funebris 209	97.1	2.4	0.5	0.0
Cupressus macrocarpa guadalupensis 211	66.3	27.9	5.7	0.0
Cupressus lusitanica 203	85.2	14.8	0.0	0.0
Cupressus sempervirens 209	86.1	13.9	0.0	0.0
Chamaecyparis thyoides 201	94.5	5.5	0.0	0.0
Chamaecyparis nootkatensis 209	91.4	8.6	0.0	0.0
Chamaecyparis obtusa 213	91.5	8.5	0.0	0.0
Chamaecyparis lawsoniana 156	98.7	1.2	0.0	0.0
Chamaecyparis pisifera 205	79.0	5.9	14.6	0.5
Juniperus chinensis 204	90.2	9.8	0.0	0.0
Thuja plicata 218	99.0	1.0	0.0	0.0
Taxus cuspidata 205	100.0	0.0	0.0	0.0
Cephalotaxus harringtoniana drupaceae 210	100.0	0.0	0.0	0.0

Based on these results we may conclude as follows:

1.1. Among the species studied, there are three uniform types of pollen grains: *Cryptomeria japonica* have exclusively "dubius" form with papilla, the pollen grains of *Taxus cuspidata* and *Cephalotaxus harringtoniana* var. *drupacea* are also of "dubius" type but without papilla.

1.2. Exclusively "dubius" type pollen grains occurs in the following species: *Cupressus arizonica, C. lusitanica, C. sempervirens, Chamaecyparis thyoides, Ch. nootkatensis, Ch. obtusa, Juniperus chinensis* and *Thuja plicata.* Among these species the pollen grains with papilla is scarce, below 10%: *Cupressus arizonica, Chamaecyparis thyoides, Ch. nootkatensis, Ch. obtusa, Ch. lawsoniana, Juniperus chinensis, Thuja plicata.*

2. Beside the "dubius" forms the pollen grains of "hiatus" type also occurs.

2.1. The "dubius" form is dominant, the quantity of the pollen grains of "hiatus" type is very low or always below 10%: *Taxodium mucronatum, Cupressus funebris, C. macrocarpa guadalupensis.* In the case of *T. mucronatum,* the quantities of the pollen grains with papilla, and without papilla are equal. The "dubius" type without papilla is the dominant at *C. funebris* and *C. macrocarpa.*

2.2. Beside the "dubius" form, the "hiatus" also occurs in significant per cent; *Sequoia sempervirens, Chamaecyparis pisifera.*

B) TRANSMISSION ELECTRONMICROSCOPICAL RESULTS *Sequoia sempervirens* (LANB.) ENDL. (Plate V, fig. 1, 2)

The exine consists of ectexine and endexine, this later mentioned layer is 2 or 3 times thicker than the ectexine. The outer layer of the ectexine is the thickest, its surface is inequal and covered by granules with strong electron scattering power, which are probably pollenkitt origin. The infratectal layer is granular, narrow, the thickness of the foot layer is equal with the infratectum, T/I/F=4–6/1/1. The endexine, under the foot layer consists partially of unit membranes ("a" layer), under this there are the "b" layer with sparse lamellae. Taking into consideration the earlier data (UENO 1959, 1960a, b), particularly the publication of GULLVAG (1966) the lamellae are not composed by granules. The fine structure of the endexine was cleared by the present investigations. In comparison with the data of M. VAN CAMPO and LUGARDON (1973) the ectexine of *Sequoia sempervirens* is the most similar to those of *Cupressus arizonica,* the endexine to those of *Agathis alba.* We emphasize, that based on our own results, the granular infratectal layer with tectum may break easily and because of this fact, several SEM data must be regarded with criticisms.

C) SCANNING ELECTRON-MICROSCOPICAL RESULTS

Among the data of the literature we emphasize the following: TAKEOKA (1965), p. 65: "8 different types of orbicules were first detected by the writer an electron-microscope on the pollen grains surface of coniferae (1956—1964). The type of orbicules is one of the features of individual genera, and is useful for the classification of genera." HO and SZIKLAI (1973), p. 17: "Fine structure of the pollen surface from five species of the *Taxodiaceae* family and one species of the *Cupressaceae* family was studied by scanning and transmission electron microscopy. All samples investigated have the same microverrucate sculpture. *Sciadopitys* is an exception, having a micro-echinate pattern."

The results of the present investigations may be summarized as follows:

1. *Sequoia sempervirens* (LANB.) ENDL. (Plate VI, fig. 1—6)

On the deepened part of the proximal surface it is a characteristic papilla (Plate VI, fig. 1, 2). The surface of the papilla is covered by small granules (Plate VI, fig. 3, 4), the proximal surface and those of the equatorial area is rugulate, but on these elements are also small granules. The distal surface is granular, these granules anastomose often (Plate VI, fig. 6). The orbiculi are covered by tiny coni.

2. *Sequoia gigantea* TORR. (Plate VII, fig. 1—4)

The proximal part deepens, the papilla is great. Similarly to the previous species the surface of the papilla is also granular, the proximal is rugulate (Plate VII, fig.

3, 4). The granules of the distal pole generally do not anastomose often coni occurs also. The orbiculi are smaller than those of *Sequoia sempervirens,* and its surface is covered with tiny spinae (Plate VII, fig. 4).

3. *Taxodium distichum* (L.) RICH. (Plate VIII, fig. 1, 2)

Following the paper of LIEUX (1980), p. 22: "Exine thin, ca. 1 μm thick, apparently tectate, gemmate; nanno-gemmae (< 1 μm in diameter)...". The surface ornamentation of this species is especially similar to *S. gigantea.* The rugulate surface is characteristic on the polar part.

4. *Taxodium mucronatum* TENORE (Plate VIII, fig. 3—5)

The fine sculpture of this species differs from the above discussed species. Around the papilla the surface is less rugulate and there are granular forms transitional to the orbiculi (Plate VIII, fig. 3, 4). Essentially this is characteristic to the distal surface and to the equatorial area.

5. *Cryptomeria japonica* (L. F.) DON. (Plate IX, fig. 1—5)

Around the papilla, the proximal surface is finely granular (Plate IX, fig. 1, 4). The equatorial area, and the distal surface is granular or covered with tiny coni. Moreover larger granules or rugulate ornamental elements also occur, which are similar to the orbiculi or the above mentioned transitional elements (Plate IX, fig. 3, 5). The orbiculi is covered with tiny spinae (Plate IX, fig. 3, 5).

6. *Cupressus arizonica* GREENE (Plate X, fig. 1—3)

The surface is finely granulate-rugulate, the surface of the orbiculi is granular coni were not observed during the present investigations.

7. *Cupressus funebris* ENDL. (Plate X, fig. 4—6)

In contrast to the previous species, the surface is mostly finely rugulate this kind of ornamentation is not always the same of the different part of the pollen surface. (Plate X, fig. 5, 6), but this may be in consequence of the method of preparation. The surface of the orbiculi is covered with tiny coni (Plate X, fig. 5).

8. *Cupressus macrocarpa* HARTW. var. *macrocarpa* (Plate XI, fig. 1—4)

The surface is finely granular (Plate XI, fig. 2, 3) sometimes the ornamental elements anastomose (Plate XI, fig. 4). The orbiculi are ornamented by characteristic coni (Plate XI, fig. 2).

9. *Callitris cupressiformis* VENT. (Plate XI, fig. 5, 6)

The surface is often granular or covered with tiny coni but often the ornamentation described at *Taxodium mucronatum* and *Cryptomeria japonica* occurred at this species too. (Plate XI, fig. 6). The orbiculi are covered by coni.

Plate I

1—12. *Sequoia sempervirens* (LANB.) ENDL. ×1000

Plate II

1—6. *Taxodium mucronatum* TENORE
7—12. *Cryptomeria japonica* (L. F.) DON. ×1000

Plate III

1—4. *Cupressus arizonica* GREENE
5—9. *Cupressus funebris* ENDL.
10—16. *Cupressus macrocarpa* HARTW. var. *guadalupensis* MASTERS
17—20. *Cupressus lusitanica* MILL.
21—24. *Cupressus sempervirens* L.
25—28. *Chamaecyparis thyoides* (L.) SARGENT
29. *Chamaecyparis nootkatensis* (LANB.) SPACH ×1000

Plate IV

1—3. *Chamaecyparis nootkatensis* (LANB.) SPACH
4—7. *Chamaecyparis obtusa* ENDLICHER
8—10. *Chamaecyparis lawsoniana* (MURR.) PARL.
11—13. *Chamaecyparis pisifera* SIEB. et ZUCC.
14—19. *Juniperus chinensis* L.
20—23. *Thuja plicata* DON.
24, 25. *Taxus cuspidata* SIEB. et ZUCC.
26, 27. *Cephalotaxus harringtoniana* K. KOCH var. *drupaceae* KOIDZ ×1000

Plate V

1, 2. *Sequoia sempervirens* (LANB.) ENDL., T = tectum, I = infratectum, F = foot layer, a = the outer layer of the endexine, b = the inner layer of the endexine, ×50 000

Plate VI

1, 2. *Sequoia sempervirens* (LANB.) ENDL., ×2000
3—6. *Sequoia sempervirens* (LANB.) Endl., ×10 000

Plate VII

1, 2. *Sequoia gigantea* TORR., ×2000
3, 4. *Sequoia gigantea* TORR., ×10 000

Plate VIII

1. *Taxodium distichum* (L.) RICH., ×2000
2. *Taxodium distichum* (L.) RICH., ×10 000
3. *Taxodium mucronatum* TENORE, ×2000
4, 5. *Taxodium mucronatum* TENORE, ×10 000

Plate IX

1, 2. *Cryptomeria japonica* (L. F.) DON., ×2000
3—5. *Cryptomeria japonica* (L. F.) DON., ×10 000

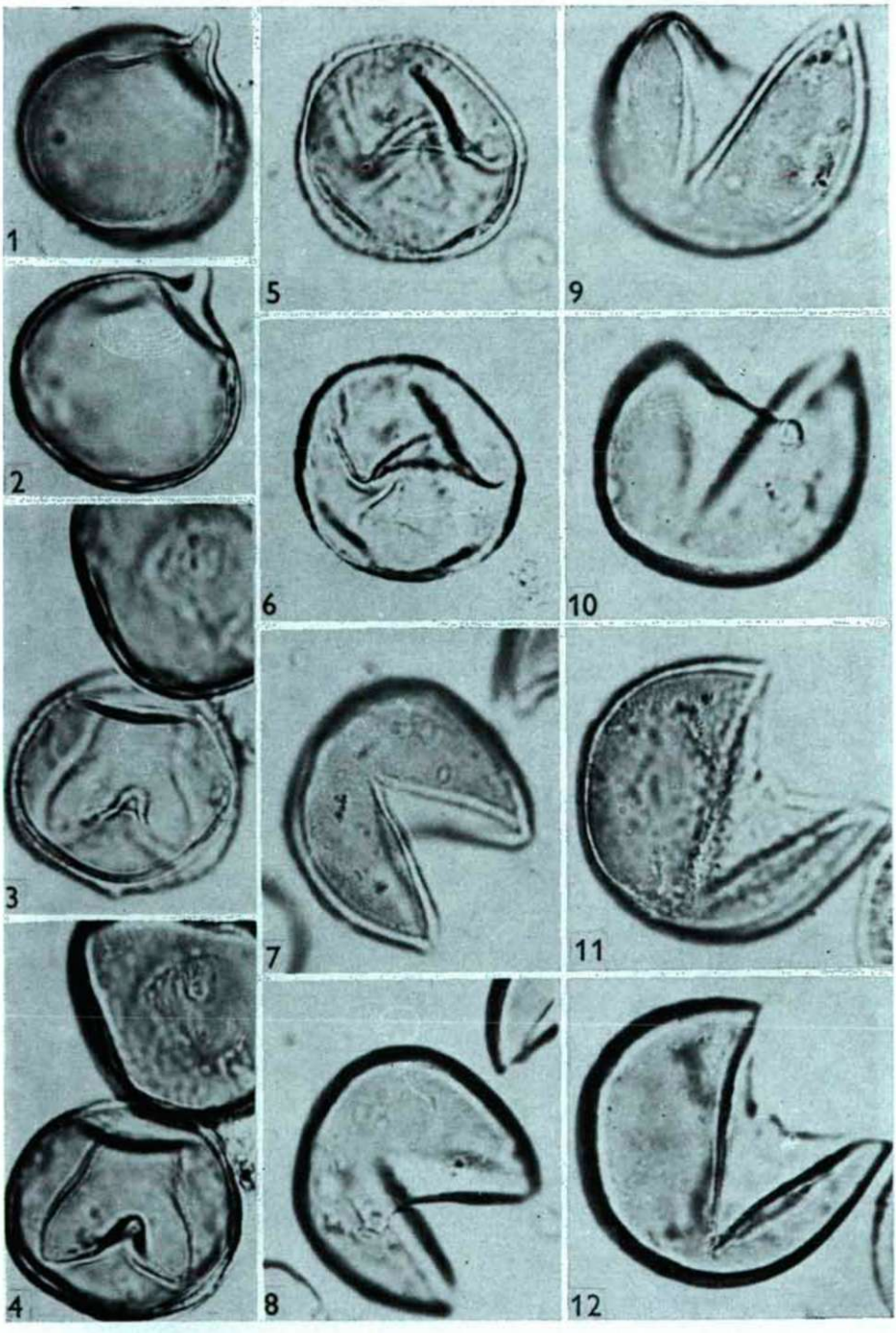
Plate X

1. *Cupressus arizonica* GREENE, ×2000
2, 3. *Cupressus arizonica* GREENE, ×10 000
4. *Cupressus funebris* ENDL., ×2000
5, 6. *Cupressus funebris* ENDL., ×10 000

Plate XI

1. *Cupressus macrocarpa* HARTW. var. *macrocarpa*, ×2000
2—4. *Cupressus macrocarpa* HARTW. var. *macrocarpa*, ×10 000
5. *Callitris cupressiformis* VENT., ×2000
6. *Callitris cupressiformis* VENT., ×10 000

Plate I



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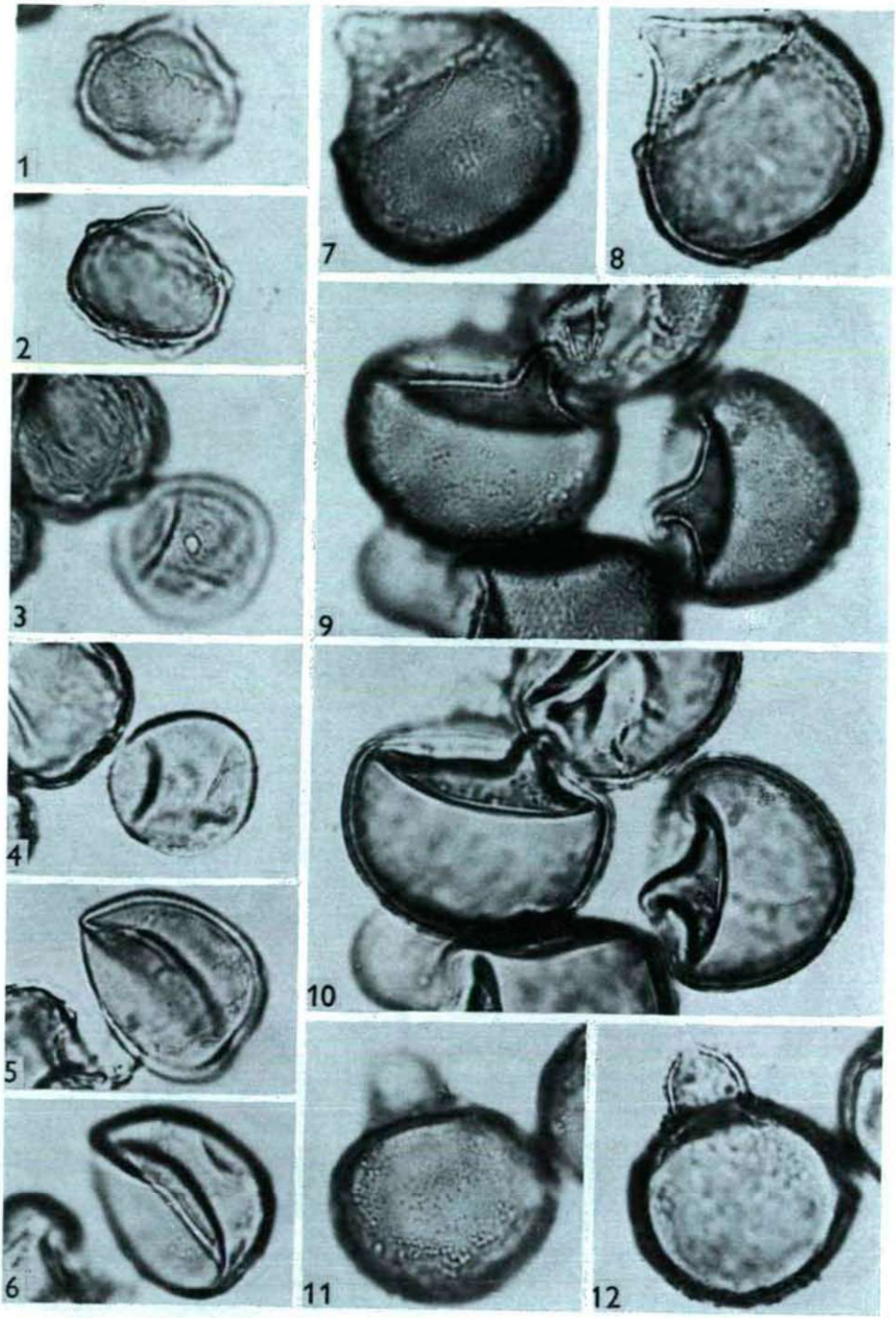

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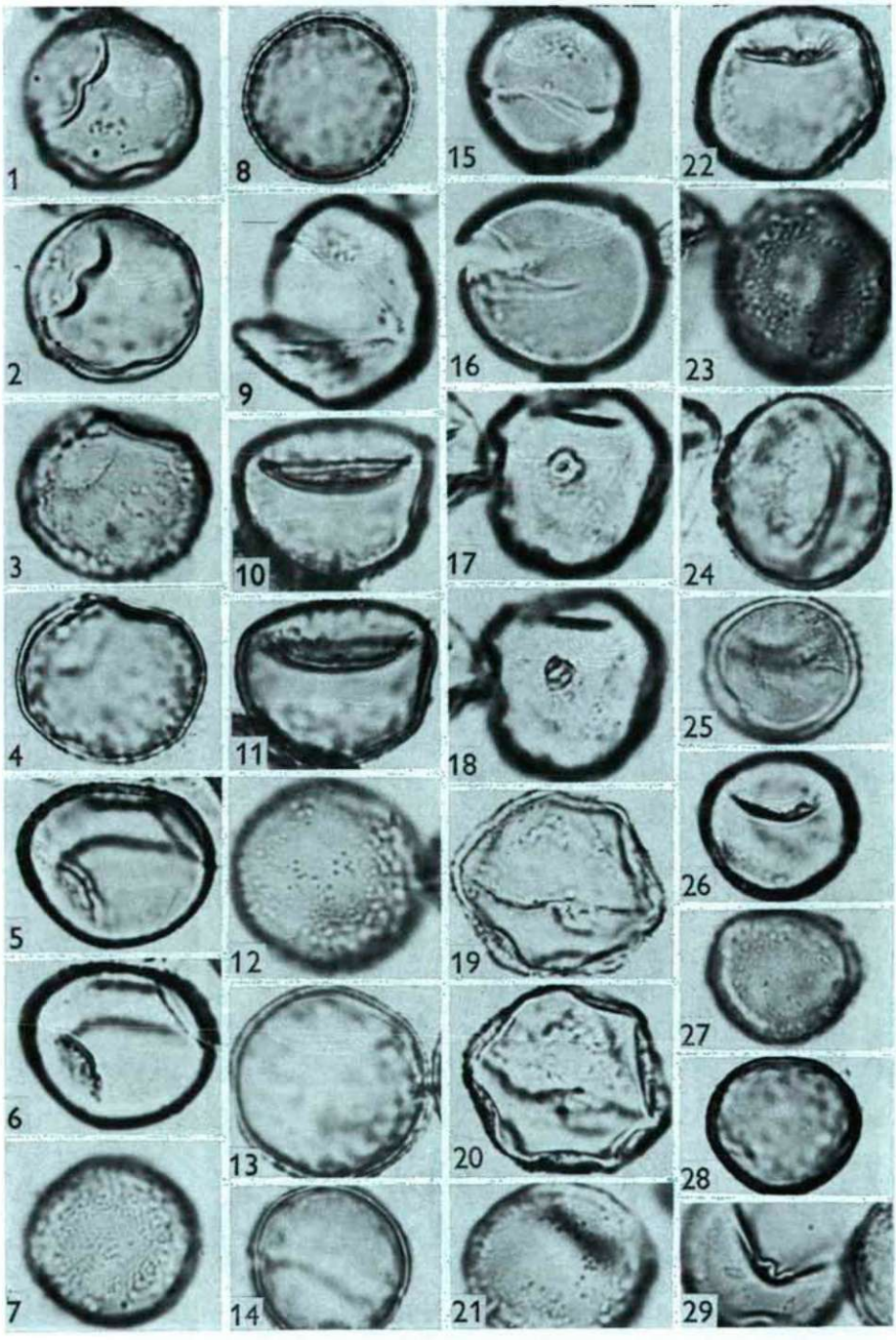

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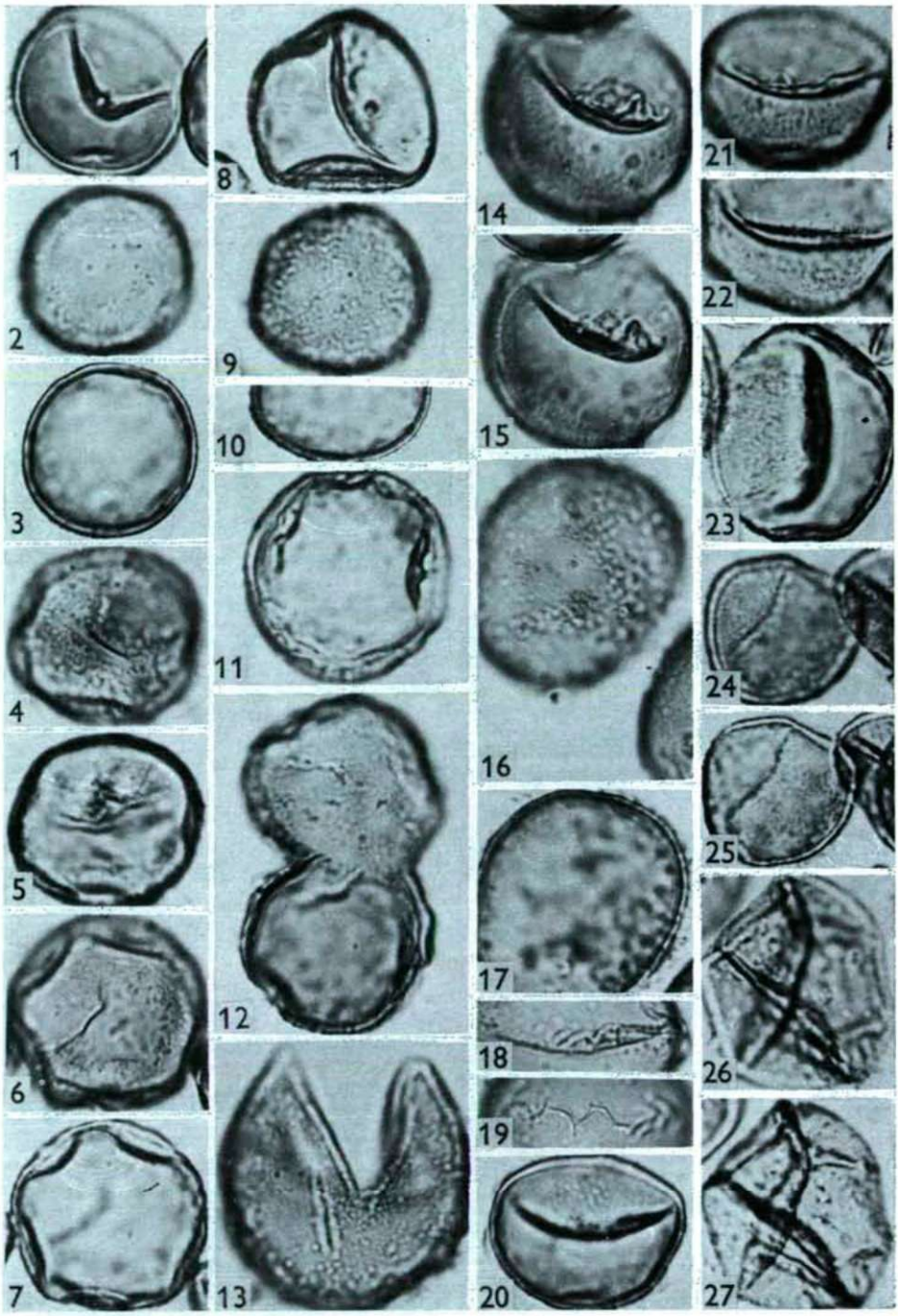


Plate V

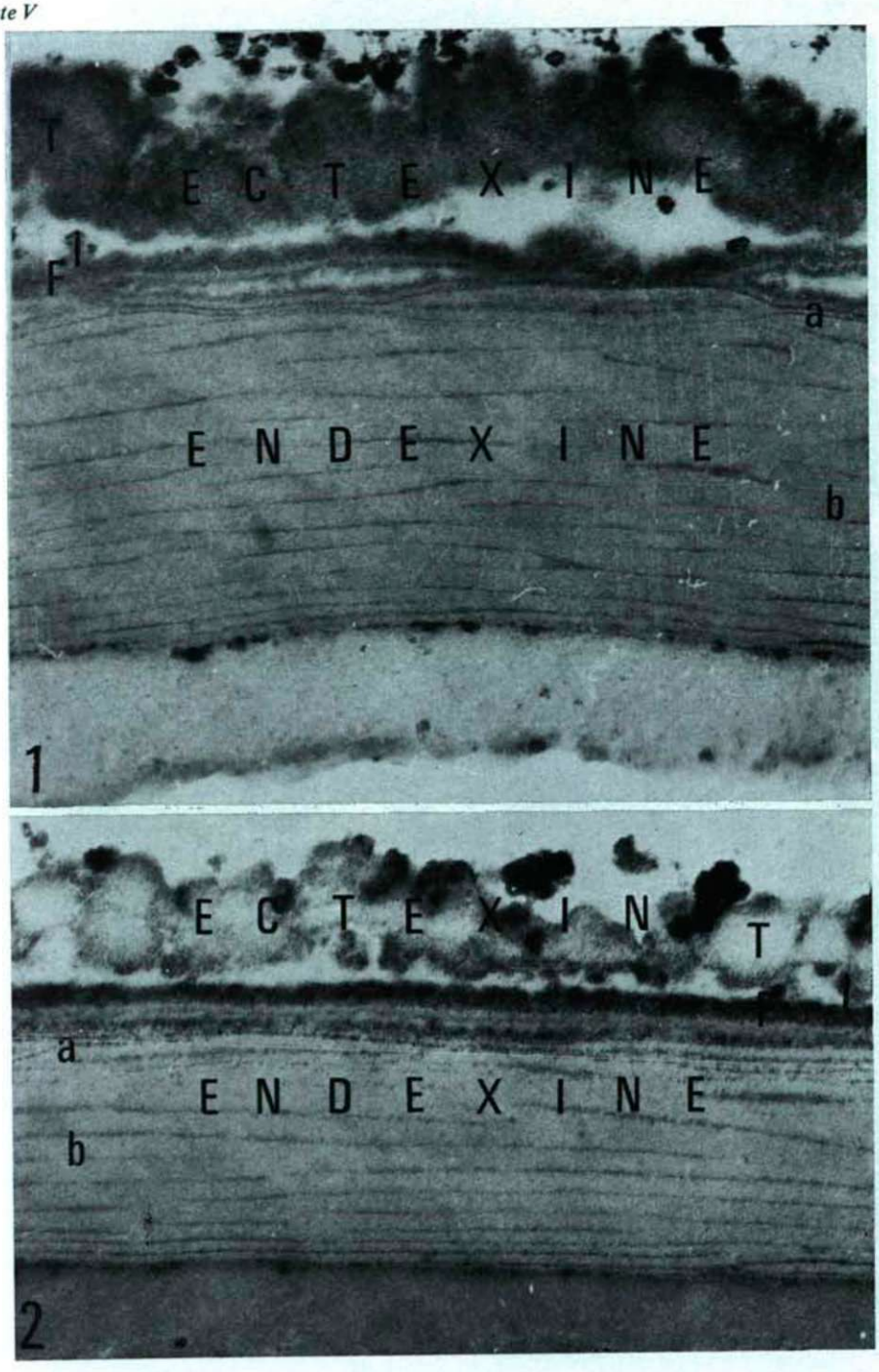
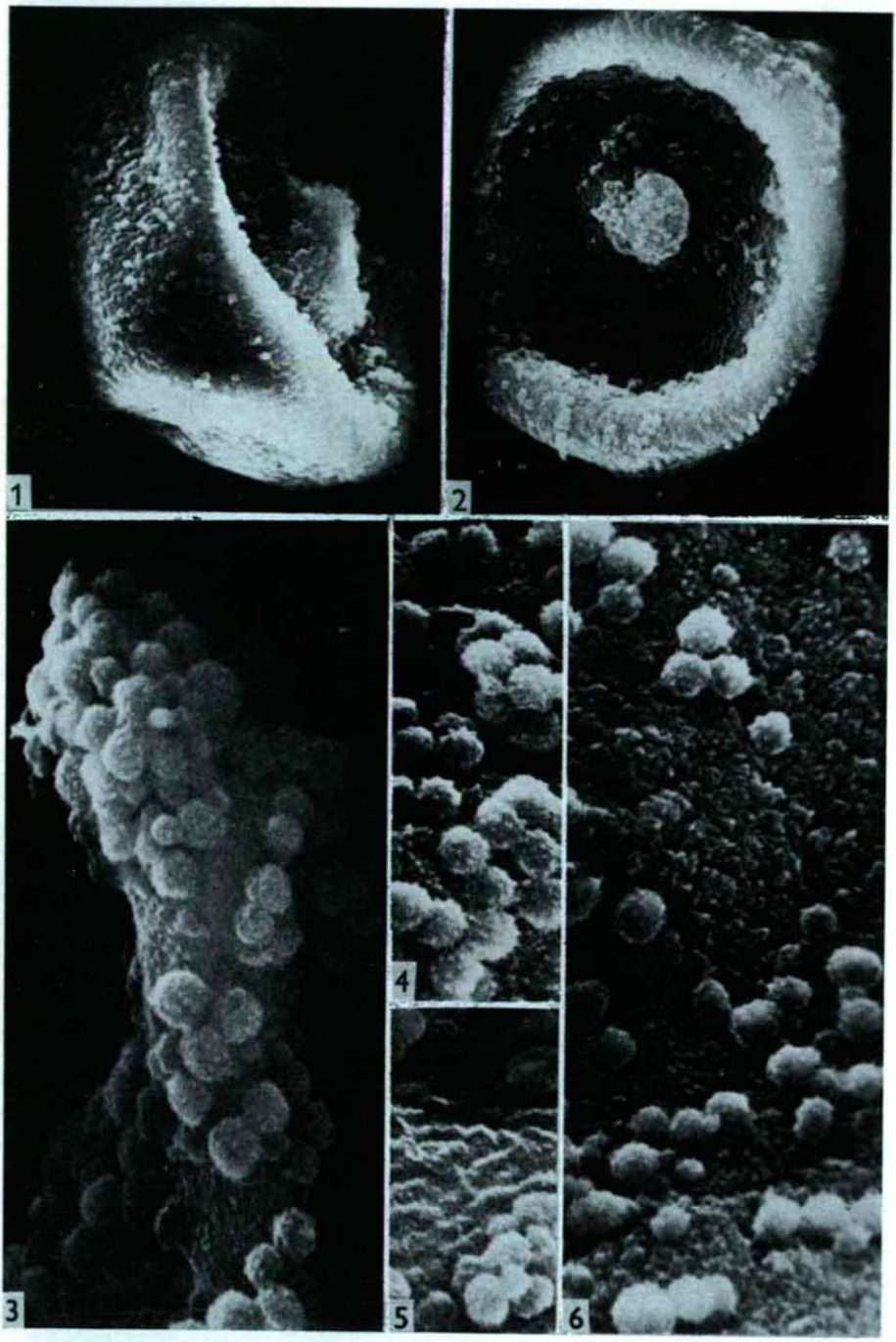


Plate VI



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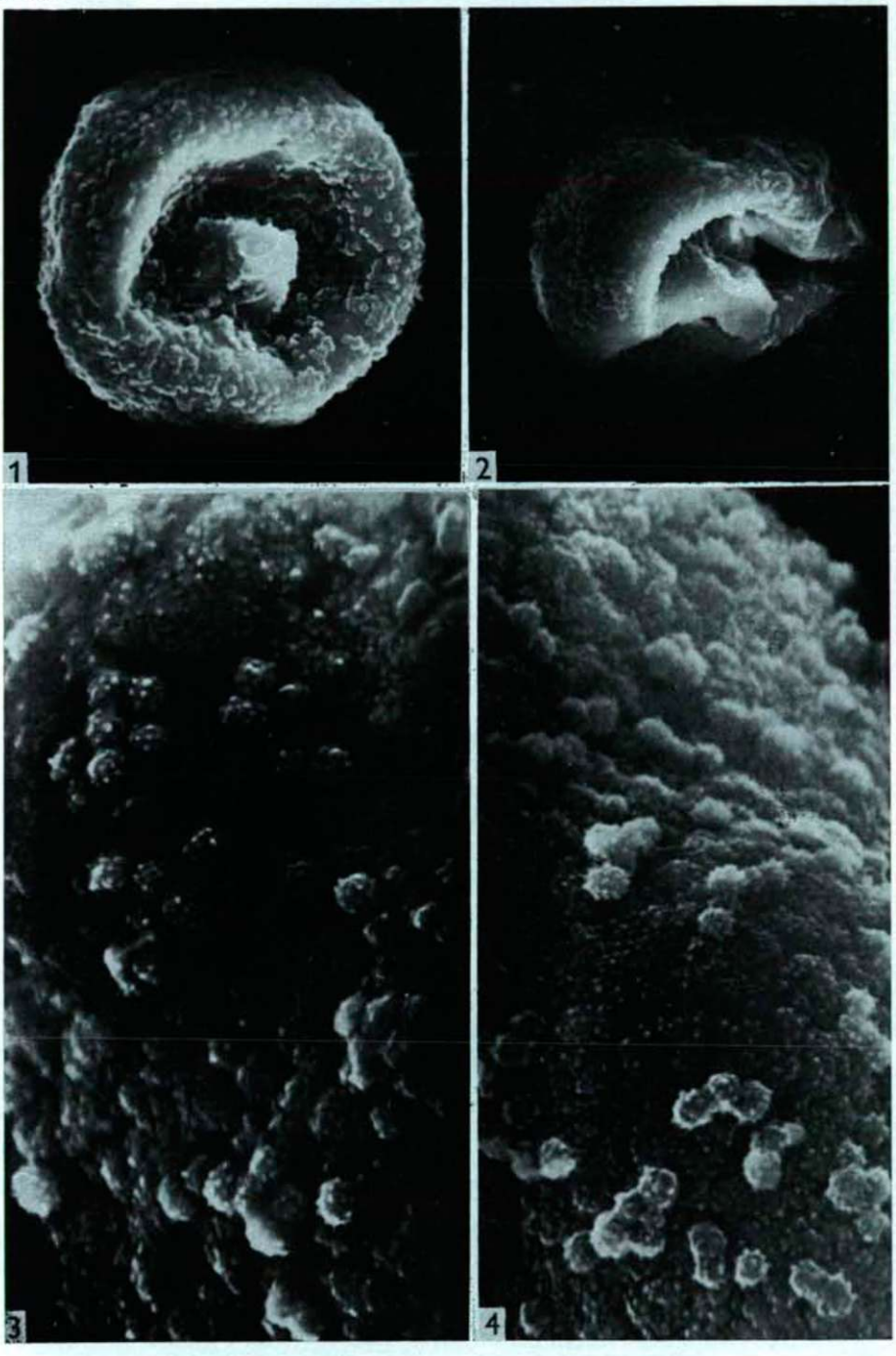


Plate VIII

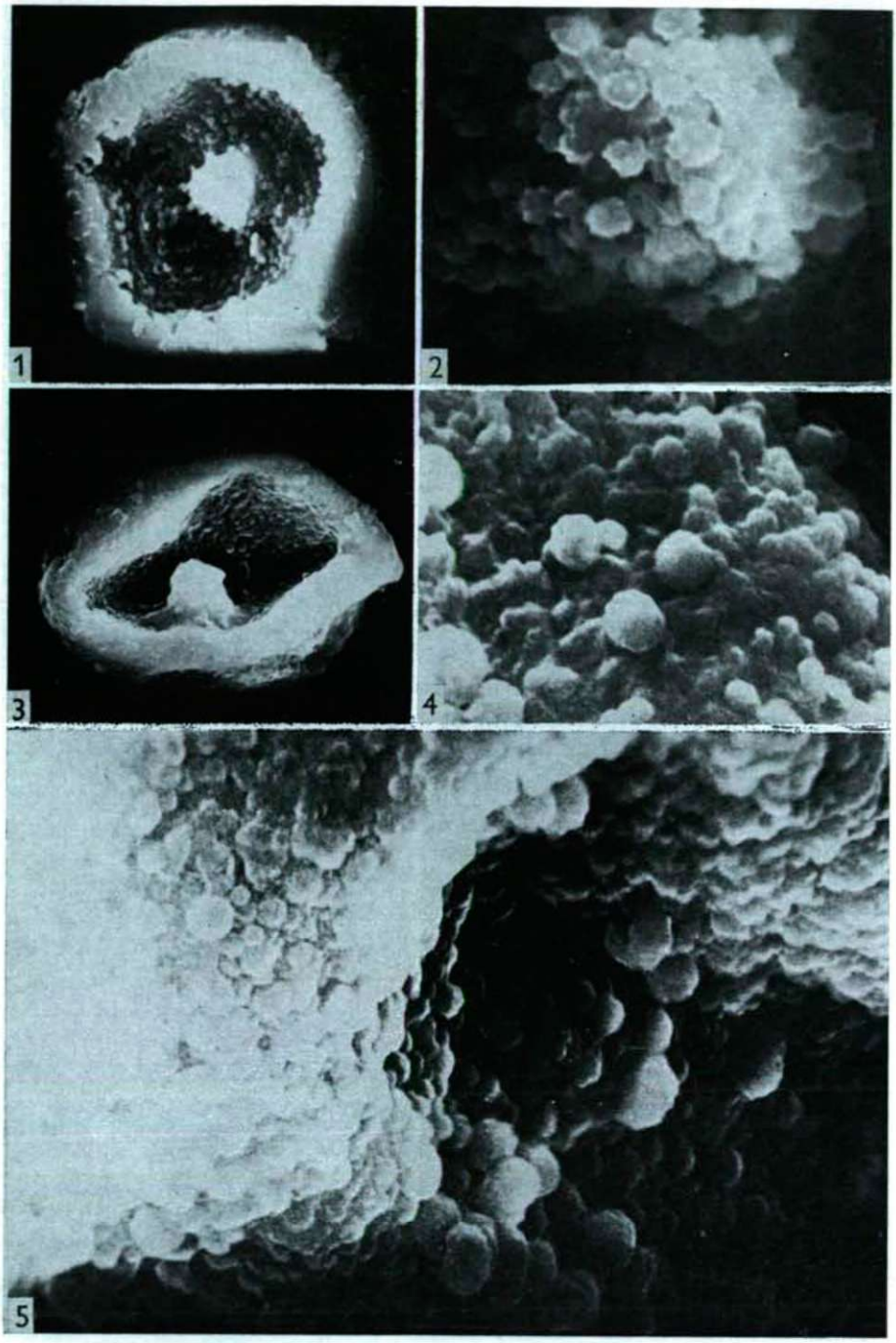


Plate IX

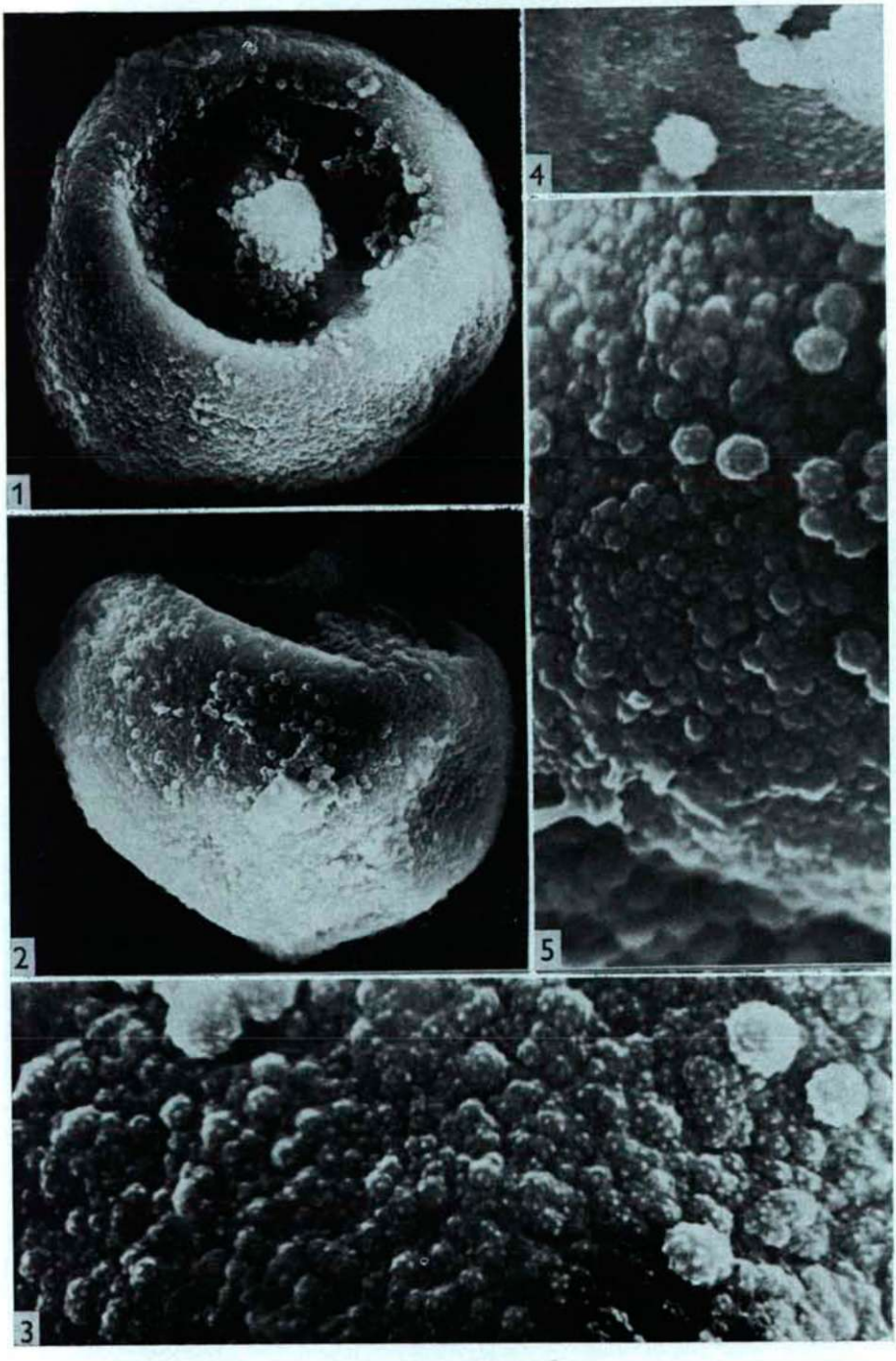


Plate X

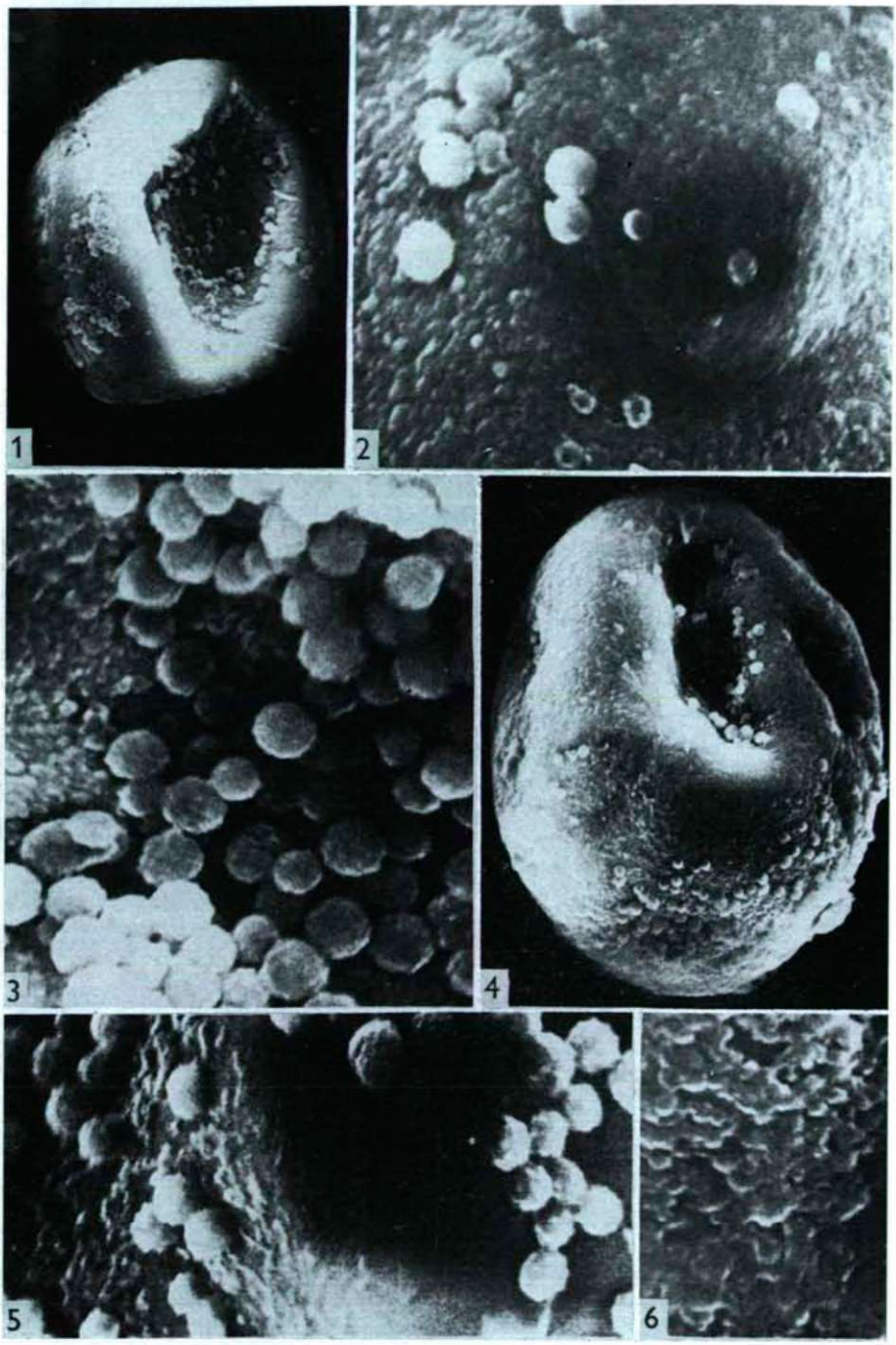
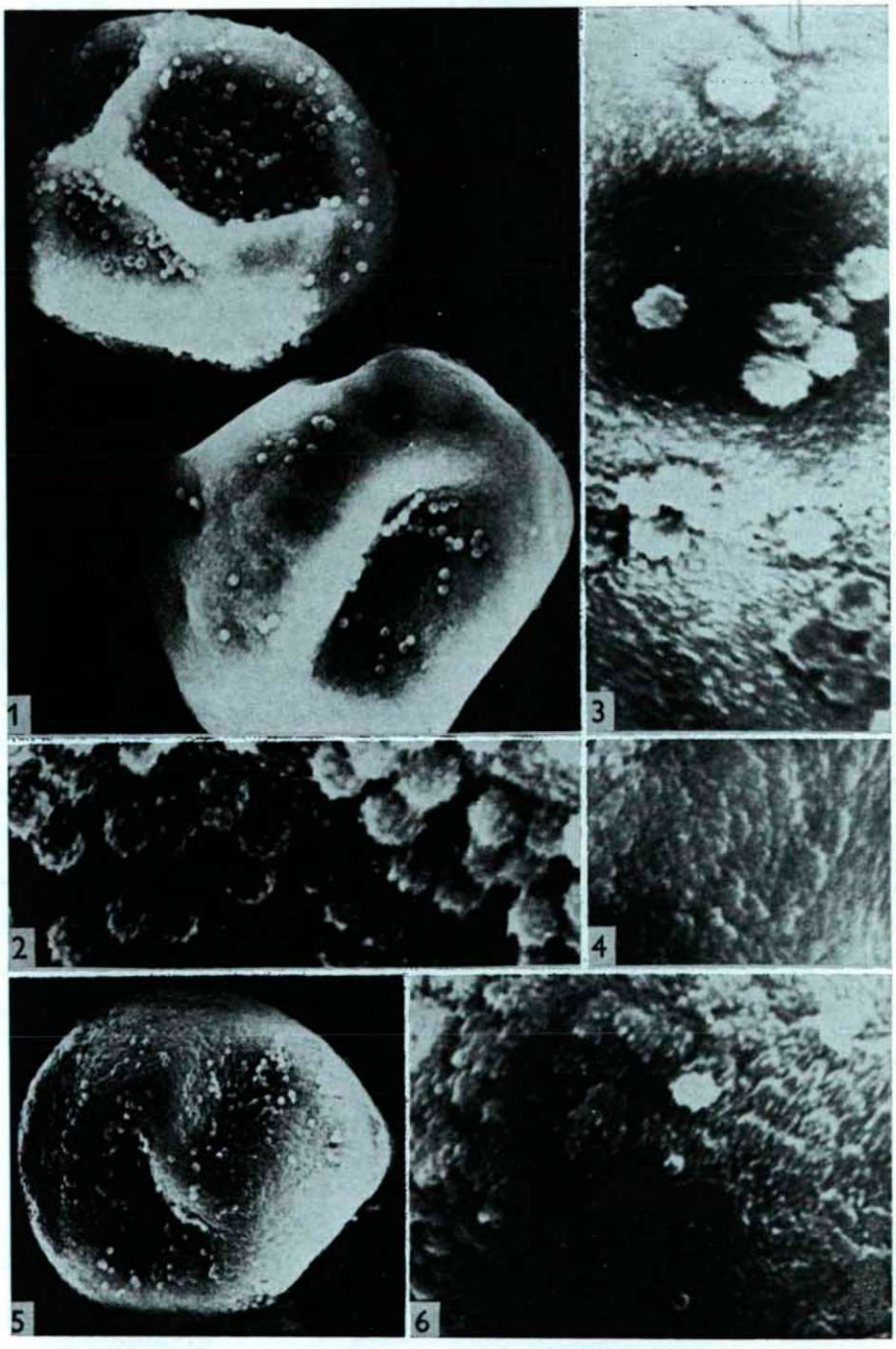


Plate XI



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COMPARATIVE STUDY OF ALBIAN MONOSULCATE ANGIOSPERM POLLEN GRAINS

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Abstract

Authors reviewed the diagnosis of the monosulcate and trichotomosulcate pollen of the early angiosperms in order to clear their nomenclatural problems and on the basis of their own material, revaluated the status of *Clavatipollenites, Retimonocolpites* and *Liliacidites*. Four new genera: *Brenneripollis* gen. nov., *Harskutipollis* gen. nov. and *Singhipollis* gen. nov. *Foveomonocolpites* gen. nov. are proposed. Nine new species are described and several new combinations are suggested. A new system for the early angiospermous pollen grains is proposed.

Key words: Palynology, Middle Cretaceous, angiosperm pollen, pollen taxonomy.

Introduction

Well-documented angiosperm pollen from the Cretaceous are important evidences of the time of appearance and adaptive radiation of the angiosperms. MULLER (1968), VAN CAMPO (1971), VAN CAMPO and LUGARDON (1973), DOYLE, VAN CAMPO and LUGARDON (1975) discovered the criteria distinguishing the most ancient angiospermous monosulcate pollen from the similarly monosulcate gymnospermoid ones.

The authors suppose that the Hungarian Albian-Cenomanian sediments have a significant role in the cognition of the early angiospermoid monosulcate pollen. The exact age of these layers is proved by geological and paleontological data (JUHÁSZ, 1983). In the different lithological formations of the Albian appeared in a great profusion of forms although not in a great number, all the monosulcate and tricolpate-tricolporoidate pollen types which are described from different sites of the world from the Barremian on. In addition to this, several new genera and new species were found in the authors'material. Their systematic description started not long ago (GÓCZÁN and JUHÁSZ, 1984; GÓCZÁN and JUHÁSZ, 1985; and this work as well.)

In this work the authors review the status of the monosulcate and trichotomosulcate angiosperm pollen which were classified by other authors into the formgenera *Clavatipollenites, Retimonocolpites, Liliacidites, Peromonolites, Asteropollis, Trichotomosulcites*. A great aid was given to us WALKER's (1976 a, b) publications. His study of 230 genera and 1000 species of recent primitive ranalean angiosperms greatly promoted understanding the aperture types of the pollen and the architecture of the pollen-walls.

The thickness of the nexine inside exine was considered to be a significant character in the systematic grouping the monosulcate-trichotomosulcate species. Several

forms has a characteristically thick or thin nexine which clearly separates them. In the descriptions of the pollen in the case of size the principles of LAING (1975, p. 779) and in the case of form and dimension that of WALKER and DOYLE (1975) were followed.

Systematic part

Genus: **Brenneripollis** gen. nov.

Synonyms: *Peromonolites* BRENNER 1963 (partim)
Liliacidites COUPER 1953 (partim)
Retimonoculpites PIERCE 1961 (partim)
Arecipites WODEHOUSE 1933 (partim)

Derivatio nominis: denominated after the palynologist G. J. BRENNER.
Type species: *Brenneripollis pellitus* gen. nov. et sp. nov.
Genusdiagnosis: Small and medium-sized, thin walled, monosulcate, tectate-reticulate pollen; the irregular reticulum of the sexine is often only loosely connected with the nexine. The sulcus is a simple, narrow slit, in most cases reaches from pole to pole with pointed extremities, it opens in the sexine and nexine in an identical form, although often not in the same level. The nexine is smooth, the sexine is reticulate. The infratectum of the sexine consists of bacula emerging to different heights from the nexine while the tectum consists of muri connecting the often thickened outer ends of the bacula, forming an irregularly shaped reticulum. The surface of the muri is often ornamented with coni or verrucae. Into this formgenus allocated as follows:

Brenneripollis pellitus gen. nov. et sp. nov.
Brenneripollis gracilis sp. nov.
Brenneripollis surensis sp. nov.
Brenneripollis peroreticulatus (BRENNER 1963) comb. nov.
Brenneripollis reticulatus (BRENNER 1963) comb. nov.
Brenneripollis tectus (NORRIS 1967) comb. nov.

Differential diagnosis: The sexine loosely connected with the nexine separates well *Brenneripollis* gen. nov. from the other thin-walled, tectate-reticulate, monosulcate pollen genera. So it differs from the closely related genus *Retimonocolpites* PIERCE 1961, which has a regular reticulum of uniform mesh size the lumina being uniformely distributed over the surface. The sexine of *Liliacidites* COUPER 1953 is closely connected with the nexine and the diameter of the lumina of the reticulum tends to diminish from the central part towards the poles.

Remarks: The characteristic reticulum of *Brenneripollis* gen. nov. and the relation of sexine/nexine, unambiguously distinguishes it from the other tectate-reticulate monosulcate genera. According to the authors these characters are sufficient and necessary to suggest the introduction of *Brenneripollis* gen. nov. for the fossil monosulcate pollen grains which are similar to *Peromonolites peroreticulatus* and *Peromonolites reticulatus*, described by BRENNER (1963) as new species from the Potomac Group of Maryland and which was considered by SINGH (1971) as *Liliacidites*, by DOYLE et al. (1975) as *Retimonocolpites*, and by JUHÁSZ and GÓCZÁN (1976) as *Arecipites*.

Brenneripollis pellitus gen. nov. et sp. nov.
(Plate I., Figs. 1—20)

Synonym: *Retimonocolpites* cf. *reticulatus* (BRENNER 1963) comb. nov.
DOYLE et al., 1975., p. 456., Pl. 5., Figs. 5—8.

Derivatio nominis: pellitus (Latin)=long-haired. The name refers to the sexine covering the nexine as a fur-coat.
Locus typicus: Súr, Borehole Súr-1., Mts Bakony.
Stratum typicum: 535.0—538.5 m. Tés Clay Formation, Middle Albian.
Holotype: Súr-1.: 535.6/2. Coordinates: 5.5-94.8. Plate I., Figs. 1—20.
Diagnosis: In polar view globose-euprolate, small and medium-sized monosulcate, tectate-reticulate pollen; the sexine is loosely connected with the nexine. Sulcus simple, narrow slit from pole to pole which opens in identical form in the sexine and in nexine. The nexine is about 1 μm thick, smooth, unstructured, decidedly separated from the sexine. The sexine is about 2 μm thick and structured. The columella layer of the infratectum is composed of 1.6—1.8 μm high, irregularly spaced bacula. The tectum consists of 0.3—0.6 μm wide muri connecting the ends of the bacula to an irregular reticulum. The surface of the muri is ornamented with microverrucae and coni which are smaller than 0.1 μm and are densely spaced. The reticulum is irregular, it covers the entire surface, diameter of the lumina of the microreticulum is 1.8—2.8 μm.

Dimensions: Polar diameter (PD): 20 μm, equatorial diameter (ED): 18 μm, length of the inner body (LB): 16 μm, breadth of the inner body (BB): 14 μm, exine thickness (et): 3 μm, sexine thickness (st): 2 μm, nexine thickness (nt): 1 μm, PD:ED=1.17, PD:et=6.6, st:nt=2, PD:re=7.1-11.1 (re=diameter of reticulum)

Differential diagnosis: *Brenneripollis pellitus* sp. nov. differs from the closely related *Brenneripollis reticulatus* (BRENNER 1963) comb. nov. by the smaller size and by the reticulum with lumina of larger diameter. From similarly sized *Brenneripolllis peroreticulatus* (BRENNER 1963) comb. nov. it differs by the reticulum with smaller lumina and by the ornaments of the muri. These two characteristics and the smaller size differentiate it from *Brenneripollis tectus* (NORRIS 1967) comb. nov. as well.

Remarks: Authors have the opinion that the specimen described by DOYLE et al. (1975, p. 146,., Pl. 5., Figs. 5—8) as *Retimonocolpites* cf. *reticulatus* (BRENNER 1963) comb. nov. (despite the 1—2 μm differences in size) can be sooner identified with *Brenneripollis pellitus* sp. nov. than with BRENNER's *P. reticulatus* — especially when the ultrastructure of the muri is also considered.

Occurrence: Transdanubian Central Range (Hungary): Tés Clay Formation, Middle Albian.

Brenneripollis gracilis sp. nov,
(Plate I., Figs. 21—42.)

Synonyms: *Liliacidites tectus* NORRIS, 1967, Pl. 16., Figs. 22—23.
Liliacidites tectus NORRIS, 1967; in SINGH, 1971, p. 190.
Pl. 29., Figs. 1—4.

Derivatio nominis: gracilis (Latin)=gracile.
Locus typicus: Tés, Borehole Tt—27., Mts Bakony.
Stratum typicum: 38.5 m, Tés Clay Formation, Middle Albian.
Holotype: Slide 35.5/2, coord. 4.3—105.4. Plate I., Figs. 21—42.

Diagnosis: In polar view globose-euprolate, small and medium-sized, monosulcate, tectate-reticulate pollen; the sexine of which is loosely connected with the nexine. The sulcus is a simple, narrow slit extending from pole to pole and tapered at both ends. It widens out sometimes in the central field and it opens in the sexine and in the nexine in the same level. The nexine is smooth, less than 1 μm thick, often it is similar to a body tending to separate in different degree from the sexine. Sexine thickness is between 0.8—1.8 μm and it has a reticulate structure. The columella consists of 0.8—1.8 μm high and 0.3—0.5 μm thick bacula spaced 1—2 μm apart, while the tectum consists of less then 1 μm thick muri connecting the ends of the bacula into an irregular reticulum. The reticulum covers the whole surface. Diameter of its lumina: 1—2 μm.

Dimensions: PD: 19—24 μm., ED: 12—16 μm, LB: 15—18 μm, BB: 9—12 μm, height of bacula about 0.8—1.8 μm, diameter of lumina of reticulum (re): 1—2 μm. PD:ED=1.6, PD:et=8.7—11.7, st:nt=2.4—3.6, PD:re=12—18.

Differential diagnosis: The new species is well differentiated from the other *Brenneripollis* species by the elongate-elliptical outline, the exine structure and the PD/ED index.

Remarks: Among the pollen grains described as *Liliacidites tectus* nov. sp. by NORRIS (1967) the specimens presented on Pl.16. Figs. 22—23. are closer related to *Brenneripollis gracilis* sp. nov. than to the type of *L. tectus* regarding form, dimensions, exine stratification. SINGH (1971) also published pollen which he considered as *Liliacidites tectus* NORRIS 1967 (Pl. 29., Figs. 1—4.) These are sooner *Brenneripollis gracilis* than *tectus*.

Occurrence: Transdanubian Central Range, Tés Clay Formation, Middle Albian.

Brenneripollis peroreticulatus (BRENNER 1963) comb. nov.
(Plate II., Figs. 1—15.)

Type and diagnosis: *Peromonolites peroreticulatus* n. sp., BRENNER, 1963, p. 94., Pl. 41., Figs. 1a-b.

Remarks: The specimen from the Lower Cenomanian of Pénzeskút Marl Formation is identical with the type species in form and structure, only it is 2—3 μm bigger. Pollen grains were published since BRENNER (1963) as species *peroreticulatus* by SINGH (1971, p. 188, Pl. 28, Figs 6—11), LAING (1975, p. 780, Pl. 93, Figs. 2—5), JUHÁSZ and GÓCZÁN (1976, p. 38, Pl. 1, Fig. 22), NORVICH and BURGER (1976, p. 146, Pl. 29, Figs. 9—13), DOYLE et al. (1977, p. 461., 462., Pl. 2, Figs. 7—8), MORGAN (1980, p. 38, Figs. 10, 15). Comparing these with the type species or with the specimens collected from the type layer it can be established that the large part of pollen grains from the Albian and Lower Cenomanian sediments does not belong to *Peromonolites peroreticulatus* but to one or more other species. Regarding palynostratigraphy as well as the problem of the origin of the ancient angiosperms it is a very important fact that from the Middle Cretaceous sediments of nearly all recent continents are already known (or can be expected) such monosulcate, semitectate-reticulate pollen which without any doubt belong to the relationship of this characteristic species.

Brenneripollis reticulatus (BRENNER 1963) comb. nov.
(Plate II., Figs. 16—30)

Type and diagnosis: Brenner 1963, p. 94, Pl. 41, Figs. 3, 4.

Remarks: Authors' specimens from the Middle Albian sediments of Tés Clay Formation and from the Upper Albian of the Pénzeskút Marl Fm. correspond the diagnosis of *Peromonolites reticulatus* BRENNER 1963 in form, size, and in the structure of the sulcus and reticulum. According to BRENNER the difference between *peroreticulatus* and *reticulatus* is that the generally smaller *peroreticulatus* has a reticulum with lumina of bigger diameter while the bigger-sized *reticulatus* has a reticulum with lumina of smaller diameter. BRENNER's observations were confirmed by DOYLE et al. (1975) on the basis of investigation of material collected from the type layer with the remark that there is a great variation within both groups. In the authors' material occur all variations in the relation to size of the pollen grains and the diameter of the lumina of the reticulum.

Brenneripollis surensis sp. nov.
(Plate IV., Figs. 1—12)

Derivatio nominis: denominated after the locus typicus.
Locus typicus: Súr, Borehole Súr-1.
Stratum typicum: 535.6—538.3 m. Tés Clay Fm., Middle Albian.
Holotype: Slide 535.6/1., coord. 36.0—96.8. Pl. IV., Figs. 1—12.

Diagnosis: In polar view globose-subprolate, small-sized, monosulcate, thin-walled, semitectate-reticulate pollen. The sulcus is a simple, reaching from pole to pole and opening in the sexine and in the nexine with identical form. Exine consists of a smooth, unstructured, thinner than 1.0 μm nexine and a 1.0 μm thick, structured sexine. The infratectum is composed of 0.8—1.2 μm high and 0.3—0.6 μm wide bacula spaced 0.8—1.2 μm apart. The tectum is constructed from muri thinner than 1 μm connecting the ends of the bacula to a reticulum. The reticulum is in general regularly hexagonal and covers the whole surface of the pollen grain. The diameter of the lumina is 0.8—1.2 μm, identical on the polar and on the central parts.

Dimensions: PD: 16 μm, ED: 13 μm, PD:ED=1.2, et=1.5—1.7 μm, PD:et=10, st:nt=1, PD:re=13—20.

Differential diagnosis: The new species differs from the other *Brenneripollis* species in size and proportions. It is most similar to *B. pellitus* in its contour and in the structure of the reticulum as well. Its much smaller size and much higher. PD: re value (in *B. pellitus* 7.1—11.1, in *B. surensis* 13—20) separates from this.

Remarks: *Brenneripollis surensis* sp. nov. shows the characteristics of the genus the sexine being loosely connected with the nexine, however, due to the small size this is not so conspicuous as at the bigger species.

Brenneripollis tectus (NORRIS 1967) comb. nov.
(Plate III., Figs. 1—35)

Type and diagnosis: NORRIS, 1967, p. 106, Pl. 16, Figs. 24—25.

Remarks: NORRIS (1967) mentioned in connection with *Liliacidites tectus* nov. sp. described by him that it is similar *Peromonolites reticulatus* BRENNER, but

differs from it by its wide sulcus, by its reticulum with lumina of bigger diameter and shorter pila and by a somewhat larger size. The photo of the type specimen of *L tectus* unambiguously shows the characteristics of *Brenneripollis* (reticulum of different size, sexine loosely connected with the nexine) and the lack of the determinant characteristics of *Liliacidites* COUPER 1953 (on the central part the diameter of lumina is bigger than at the poles); therefore this species can be considered as *Brenneripollis* without any doubt. The specimens on Plate 16, Figs. 22—23. and Plate 17, Figs. 1—2., presented by NORRIS (1967) are closer related to *Brenneripollis gracilis* nov. sp. than to the type of *tectus*, in the authors opinion. The authors present on Pl. III., Figs. 1—35 specimens from their material which in their opinion, can only be identified with *B. tectus* (NORRIS) comb. nov. from the *Brenneripollis* species described till now. The differences between NORRIS' diagnosis and the authors' specimens can be considered as variation within the species.

Occurrence: Vértessomló Aleurolite Formation, mamillatum zone, Lower Albian (Mts Vértes), and Tés Clay Fm., Middle Albian.

Genus: **Retimonocolpites** PIERCE 1961 emend.

Type species: *Retimonocolpites dividuus* nov. sp., PIERCE, 1961, p. 47,. Pl. III., Fig. 87;

Emended diagnosis: Medium-sized pollen grains with elliptic-subcircular contours from the polar aspect. Monosulcate, tectate-reticulate pollen, on which the delicate reticulum is more or less regular and the lumina have identical or nearly similar diameter on the whole surface. The sulcus in the sexine is a simple slit with a somewhat wider and more obscure area in the nexine. The nexine is smooth, the sexine is reticulate. The infratectum consists of identically high, uniformly spaced bacula, while the tectum consist of muri connecting the outer ends of the bacula forming a regular reticulum having lumina of more or less identical diameter throughout the whole surface.

Differential diagnosis: *Retimonocolpites* PIERCE 1961 emend. differs from the most closely related *Clavatipollenites* COUPER 1958 in the structure of the sexine. The tectum of *Retimonocolpites* consists of the muri connecting the ends of the bacula while that of *Clavatipollenites* is formed by the fused heads of clavae. It differs from *Liliacidites* COUPER 1953 and from *Brenneripollis* gen. nov. by the structure of the sexine as well: the columella layer of *Retimonocolpites* consists of uniformly spaced bacula of identical height while in case of the other two genera spacings and heights are different. Although tectum is formed by all the three genera from a reticulum, *Retimonocolpites* differs from that of the other two by its finer reticulum having lumina of the same size and equally spaced throughout the whole surface while at the other two genera the diameter of the lumina are various and their spacing is irregular.

Remarks: The diagnosis of PIERCE (1961) characterizing the genus and differentiating it from other known tectate-reticulate, monosulcate genera proved to be insufficient. Therefore the diagnosis is emended by authors as above-mentioned. On the basis of the description and Figures (Pl. III., Fig. 87) of the type species by PIERCE (1961), the literature on the subject, and of the authors' own material it seems to be evident that among the ancient angiospermous monosulcate pollen grains exists a group which differs from the genera *Liliacidites* COUPER 1953, *Clavatipollenites* COUPER 1958 as well as from *Brenneripollis* gen. nov., *Similipollis* GÓCZÁN et JUHÁSZ 1984, and *Harskutipollis* gen. nov.-as mentioned above. In the genus *Retimonocol-*

pites PIERCE 1961 emend. can be arranged the following species: most of the specimens of KEMP (1968) described as *Clavatipollenites rotundus* nov. sp.; the *Liliacidites dividuus* (PIERCE) BRENNER 1963 pollen grains of BRENNER (1963, p. 93., Pl. 40., Figs. 7—10), HEDLUND and NORRIS (1968, Pl. V., Fig. 9), the *Clavatipollenites* sp. (Pl. I., Figs. C, D, E, I) of DOYLE (1969), the specimens published as *Clavatipollenites hughesii* COUPER 1958 minutely examined and illustrated with excellent photos by DOYLE et al. (1975), moreover *Clavatipollenites rotundus* KEMP 1968 (Pl. 107., Fig. 14) from PLAYFORD's work (1971), the pollen as *Liliacidites rotundus* (KEMP 1968) comb. nov. by LAING (1975, p. 782. Pl. 9., Figs. 1—6) and the pollen identified as *Clavatipollenites* cf. *rotundus* by CHLONOVA (1977, p. 116, Pl. IX., Figs. 8—9). From these, on the new photos of 2000× magnification of type specimens of *Clavatipollenites rotundus* KEMP 1968 taken by LAING (1976, p. 24., Pl. 1., Figs. E—F), the structure of the sexine and the reticulum formed by the muri connecting the ends of the bacula can be seen most distinctly. PIERCE in the description of *R. dividuus* established that the reticulum is sometimes separated from the endexine; this might influence DOYLE putting *peroreticulatus* in this genus. In the authors' opinion this separatedness is surely not the original characteristic of the pollen grain because the columnar layer of the infratectum is not high, the separation probably occurred as the result of some mechanical pressure. This phenomenon can be frequently observed is separates of similar exemplar as well as that of other forms (e.g. on specimens of *Crassipollis* GÓCZÁN et JUHÁSZ). Enlarging the photo of PIERCE the traces of this can be seen clearly even by magnifying it to 1000×.

Retimonocolpites rotundus (KEMP 1968) comb. nov.
(Plate IV., Figs. 13—17.)

Type and diagnosis: KEMP, E. M. 1968, P. 424—426., Pl. 79. Figs. 17—19.

Remarks: From the Middle Albian sediments of Tés Clay Fm., monosulcate, semitectate-reticulate pollen grains were found which can be identified with this species on the basis of diagnosis and Figure of KEMP. The size of these specimens is smaller by some micrometers than that of the type but they fit in the variation of size of the species which were published by KEMP about reexposing and re-examining COUPER's type material. The thickness of the exine and lumina diameter corresponds to that of data published from the type, the data of sexine and nexine, however, show reciprocal values. On authors specimens the nexine is thicker and the sexine is thinner. However, KEMP (1968) also presents pollen grains having the same sexine: nexine relation: Pl. 79., Fig. 16 and p. 426. text-fig. 3.

Genus: **Harskutipollis** gen. nov.

Derivatio nominis: denominated after the place of occurrence of the type species, village Hárskút.

Type species: *Harskutipollis robustus* gen. nov. et sp. nov.

Genusdiagnosis: In polar view globose-prolate, medium-sized, thick-walled, tectate-reticulate, monosulcate pollen the nexine of which is more than twice as thick as that of the sexine. The sulcus is a simple slit extending in the longitudinal axis of the pollen grain, it pierces uniformely both layers of the exine and it does not form a field of dissolution in the nexine. The thick nexine forms most part of the exine

and a lesser extent is formed by the thin sexine. The nexine is smooth, unstructured, closely adheres to the sexine. The sexine is ornamented, tectate-reticulate. The infratectum consists of a baculate layer while the tectum of the muri connecting the outer ends of the bacula forming a reticulum. The reticulum covers the whole surface of the pollen grain, the lumen diameters are identical all over the surface.

Differential diagnosis: *Harskutipollis* gen. nov. differs from the most closely related *Retimonocolpites* PIERCE 1961, *Clavatipollenites* COUPER 1958 and *Liliacidites* COUPER 1953 by its thick exine and by the relation of sexine: nexine. The diameter of the lumina of reticulum are the same all over the surface and in this it differs from *Similipollis* GÓCZÁN et JUHÁSZ 1984 which has a thick exine but the diameters of the lumina are various. It is separated from the tectate-reticulate, thick-walled, trichotomosulcate *Oroszlanyipollis* GÓCZÁN et JUHÁSZ 1984 by the monosulcate aperture.

Harskutipollis robustus gen. nov. et sp. nov.
(Plate IV., Figs. 18—29)

Derivatio nominis: robustus (Latin)=robust, strong.
Locus typicus: Hárskút (Mts Bakony), Borehole Hk-4.
Stratum typicum: 133.7—135.1 m, grey aleurolite, Pénzeskút Marl Formation, Upper Albian.
Holotype: Slide 69-70/2, coord. 16.8-108.5. Pl. IV., Figs. 18—25.

Diagnosis: In polar view globose-prolate, medium-sized, thick-walled, tectate-reticulate, monosulcate pollen. The sulcus is a simple, long, towards the ends tapering and usually narrow slit running in the longitudinal axis which breaks uniformly through the layers of the exine and does not form a sculptured lytic area in the thick nexine. The exine is 2.8—3.0 μm thick and has an inner thicker, unstructured layer and an outer thinner ornamented one. The smooth nexine is about 2 μm thick and is closely connected to the sexine. The sexine is 0.8—1.0 μm thick, tectate-microreticulate. The infratectum consists of thick set bacula shorter than 1 μm, while the tectum is formed by muri connecting the outer ends of the bacula to a microreticulum. The reticulum covers uniformely the whole surface, the diameter of lumina is identical (0.4—0.6 μm) all over the surface.

Dimensions: PD: 26—30 μm, ED: 22—29 μm, et: 2.8—3 μm, PD:ED= 1.0—1.1, PD:et=8.6—10.7, st:nt=0.5.

Differential diagnosis: The new species is most similar to *Retimonocolpites dividuus* PIERCE 1961 and to *Retimonocolpites rotundus* (KEMP 1968) comb. nov. The thick exine, the PD:et value, and the sexine: nexine ratio well distinguishes it from both of them.

Occurrence: Pénzeskút Marl Fm, dispar-zone, Upper Albian.

Genus: **Clavatipollenites** COUPER 1958

Type species: *Clavatipollenites hughesii* nov. sp., COUPER, 1958, p. 159, Pl. 31, Figs. 21—22. New photos of type: LAING, 1975, p. 24, Pl. 1., Figs. A—B.

Remarks: Although COUPER (1958) gave differential diagnosis neither in the description of the genus nor in that of the type species, in the authors'opinion the characters of the genus are distinctly enumerated and expressed in the name of the

genus as well and therefore on the basis of these, it can easily be differentiated from the other tectate-reticulate, monosulcate genera. According to COUPER, *Clavatipollenites* is characterized by the unstructured nexine and the tectate sexine consisting of clavate elongations fusioned at their ends; this produce in topview a microreticulate structure. KEMP (1968, p. 424) emending and rewording the diagnosis of *Clavatipollenites hughesii* COUPER "... based on re-examination of specimens from COUPER's type sample" does not write about "clavae" but about bacula: "...sexine is formed of baculate projections..., which either remain discrete or fuse at their tips to form a microreticulum".

The authors consider that by this alteration KEMP essentially changed the diagnosis of COUPER. The difference between the reticulum from fused clavae and that of from muri connecting the ends of the bacula is essential and this essentiality was recognised in the diagnosis and emphasized in giving a name by COUPER. Whereas neither the observation of COUPER (1958) nor that of KEMP (1968) can be questioned, it must be accepted that on the type specimen of COUPER the reticulum is formed by fused heads of the clavae while on the specimens of KEMP by muri connecting the ends of the bacula. Their respective photos rather prove than disprove their descriptions. On the basis of these data authors took the view that into *Clavatipollenites* COUPER (1958) those tectate-reticulate, thin-walled, monosulcate grains can be arranged whose reticulum is formed by clavate projections which expand and fuse together at their tips and the lumina of the reticulum are of identical size throughout the whole surface. The tectate-reticulate, monosulcate grains of similar structure with thin nexine on which the lumina of reticulum have identical diameter but the reticulum is not formed by the fusion of the heads of clavae but by muri connecting the ends of the bacula, belong to the genus *Retimonocolpites* PIERCE 1961 emend.

Clavatipollenites hughesii COUPER 1958
(Plate V., Figs. 1—10)

Type species and diagnosis: COUPER, R. A., 1958., p. 159., Pl. 31, Figs. 21—22.

Remarks: From the Lower Albian of Vértessomló Aleurolite Fm. (Borehole Vst-5, 39.0 m), the Middle Albian of Tés Clay Fm. (Borehole Tés-27, 49.0 m) and from Upper Albian of Pénzeskút Marl Fm. (Borehole U-4, 44.0—45.0 m) authors get such monosulcate, semitectate pollen grains which on the basis of form, the structure of the sulcus and of the sexine, structure of microreticulum are considered to be identical with *Clavatipollenites hughesii* COUPER. Although due to the bad condition of the grains the essential genus characteristics of COUPER, i.e. the microreticulum consists of fused heads of clavae, cannot be unambiguously observed in light microscope, these pollen grains might be identified as *Cl. hughesii* COUPER 1958 on the basis of the dimensions given in the description and/or measured on the photos published but above all considering the diameter of the lumina of the reticulum. Between the grains considered by the authors as *Retimonocolpites* PIERCE 1961 and the grains identified as *Clavatipollenites hughesii* COUPER 1958 there is such a great similarity in form, size, in the structure of the sulcus and of the reticulum that the idea, belonging to the same formgenus, offers itself. But in the thickness of the exine and from this in the width of the "darkened zone" which follow the sulcus and first of all in the structure of the reticulum and in the diameter of the reticular lumina, the differences are so distinct that the authors consider justified to keep both genera.

Clavatipollenites minutus BRENNER 1963
(Plate V., Figs. 11—14)

Type species and diagnosis: BRENNER 1963, p. 95., Pl. 41., Figs. 8—9.

Remarks: Small-sized, very thin-walled, monosulcate pollen grains belong to this species. The clavae are often free or form an irregular reticulum.

Occurrence: They rank among the oldest angiosperm pollen grains of Hungary. In mamillatum-zone of Vértessomló Fm. they are only sporadic, in the substuderi-zone of Pénzeskút Fm. they are more frequent.

Clavatipollenites tenellis PHILLIPS et FELIX 1971
(Plate V., Figs. 15—19.)

Type species and diagnosis: PHILLIPS and FELIX, 1971, p. 466, Pl. XV., Figs. 19—21.

Remarks: Spherical, monosulcate pollen, with very slightly developed sulcus; size between 18—30 μm. The incomplete or more or less well-developed reticulum is formed by the fused heads of the clavae.

Occurrence: mamillatum-zone of Vértessomló Fm., rare. Tés Clay Fm. (Middle Albian), frequent.

Genus: **Singhipollis** gen. nov.

Derivatio nominis: named after the palynologist CH. SINGH.
Type species: *Singhipollis mircoreticulatus* gen. nov. et sp. nov.

Genusdiagnosis: Small and medium-sized, thin-walled, tectate-reticulate, trichotomosulcate pollen; amb spheroidal. Nexine unsculptured, sexine semitectate-columellate, sculpture microreticulate. Bacula spaced about 1 μm apart form a microreticulum being connected by muri. Muri regular-shaped and of uniform size all over the body. The three-armed sulcus narrowing toward the extremities reaches or almost reaches the equator. PD:et=14—19.

Differential diagnosis: *Singhipollis* gen. nov. can be easily separated from the other trichotomosulcate, reticulate angiospermous pollen by its thin exine and microreticulate surface. The semitectate-microreticulate sculpture differentiates it from the next related *Trichotomosulcites* COUPER 1953 which has also a thin exine and is also trichotomosulcate but its structure is verrucate, microgranulate- microfoveolate. *Singhipollis* gen. nov. is similar to *Oroszlanyipollis* GÓCZÁN et JUHÁSZ 1984 in outer contour and in semitectate-reticulate sexine but it differs from it by the thin exine and the sexine: nexine ratio.

Remarks: Pollen grains which can be arranged into this genus were described as *Apiculatisporites vulgaris* n. sp. by GROOT and GROOT (1962, p. 155., Pl. VI., Figs. 4—8) from the Upper Albian—Lower Cenomanian rocks of Portugal (Nazaré) and the same species was published by LAING (1976, p. 19., Pl. 2., Figs. E—F) from Middle Cenomanian rhotomangense-zone of England. SINGH (1971) described pollen grains as *Liliacidites trichotomosulcatus* nov. sp. (p. 191., Pl. 29, Figs. 5—7) which can be arranged into *Singhipollis* gen. nov. According to the authors' opinion the

structure and sculpture of the small and medium-sized, thin-walled, semitectate-microreticulate, trichotomosulcate pollen grains, moreover their narrow chronological age (from Middle Albian to Middle Cenomanian) and wide area of occurrence (Canada, England, Portugal, Hungary) justify to separate them from the apiculate pteridophyte spores as well as from the species of the monosulcate *Liliacidites* and the trichotomosulcate *Trichotomosulcites* which have nonreticulate exine. For them is suggested a new genus. The following species are transferred here to the genus

Singhipollis gen. nov.:
Singhipollis microreticulatus gen. nov. et sp. nov.
Singhipollis (al. *Apiculatisporites*) *vulgaris* (GROOT et GROOT 1962) comb. nov.
Singhipollis (al. *Liliacidites*) *trichotomosulcatus* (SINGH 1971) comb. nov.
Singhipollis (al. *Liliacidites*) *orbiculatus* (SINGH 1983) comb. nov.

Singhipollis microreticulatus gen. nov. et sp. nov.
(Plate V., Figs. 25—30)

Locus typicus: Tés, Borehole Tés-27.
Stratum typicum: 49.0 m, grey clayey-marl, Tés Clay Fm., Middle Albian.
Holotype: Slide 49/2, coord. 15.3—105.0. Plate V., Figs. 25—30.

Diagnosis: Small-sized, thin-walled, semitectate-microreticulate, trichotomosulcate pollen with spheroidal amb. The three-armed sulcus narrowing toward the extremities and reaching the equator is formed by the complete break-down of the exinal elements in the distal polar area. The exine is less than 2 μm thick. The nexine is smooth, unstructured, thinner than 1 μm. The sexine is sculptured. The infratectum is columellate, consisting of 0.5 μm high and 0.2—0.3 μm thick bacula, apart 0.3—0.4 μm. Height and distance of bacula is the same all over the surface. The tectum consists of 0.2—0.3 μm thich muri connecting the outer ends of the bacula forming a microreticulum. The diameter of the lumina in the microreticulum is identical all over the surface and do not surpasse 0.5 μm. Dimensions: Size: 16 μm, et = 1 μm, st:nt = 1.

Differential diagnosis: The new species differs from the closely related *Singhipollis vulgaris* (GROOT et GROOT 1962) comb. nov. by its smaller size, by the reticulum having lumina of smaller diameter and by the shorter and closer spaced bacula of the infratectum. The same characters differentiate it from *Singhipollis trichotomosulcatus* (SINGH 1971) comb. nov. the sides of which are more convex.

Genus: **Liliacidites** COUPER 1953 emend.

Type species: *Liliacidites kaitangataensis* nov. sp., COUPER, 1953, p. 56, Pl. 7., Fig. 97.

Emended diagnosis: In polar view irregularly boat-shaped or prolate, large and medium-sized, thin-walled, monosulcate, tectate-reticulate pollen, on which the diameters of lumina of the reticulum are larger in the central parts than at the ends. The sulcus opens in the sexine and in the nexine in an identical way, the sulcus is mostly a simple slit tapering at the ends. The nexine is smooth and the sexine is reticulate. The infratectum is formed by bacula emerging from the nexine, at the central part they stand farther from each other and are longer than at the polar parts where they are shorter and stand to each other nearer. The tectum consists of

a generally irregular reticulum which is formed by the muri connecting the sometimes swollen outer ends of the bacula. PD:et >15.

Differential diagnosis: *Liliacidites* COUPER 1953 emend. differs in the structure of its tectate-reticulate exine from the similar monosulcate angiosperm pollen *Arecipites* WODEHOUSE 1933 the sexine of which — as it was demonstrated by WODEHOUSE 1933 comparing "form and structure" of recent *Phoenix dactylifera* pollen with *Arecipites* — is tectate-microfoveolate (scrobiculate) and not reticulate. The differences between *Arecipites* and *Liliacidites* were minutely analysed NICHOLS et al. (1973). In *Clavatipollenites* COUPER 1958 the reticulum of the microreticulate sexine is formed by heads of the clavae and not by the muri connecting the ends of the bacula as in *Liliacidites*. In *Clavatipollenites* the lumina of reticulum are of identical diameter all over the surface while in *Liliacidites* they are different.

Liliacidites differs from *Retimonocolpites* by the infratectum which consists of bacula having identical height and being uniformly spaced. It differs from *Brenneripollis* gen. nov. in which the infratectum is loosely connected with the nexine and consists of different long, irregularly spaced bacula and as result of this the muri connecting their ends form an irregular reticulum having variously large lumina. It differs from *Similipollis* GÓCZÁN et JUHÁSZ 1984 in which the diameters of the lumina are also various but the diameter of the lumina diminishes dorsiventrally from the sulcus to to the proximal surface and not from the equator to the poles -as in the case of *Liliacidites*.

Harskutipolllis gen. nov. has a reticulum with lumina of identical diameter all over the whole surface and has a thick exine while the exine of *Liliacidites* is thin.

Remarks: COUPER (1953) in the genusdiagnosis of *Liliacidites* did not express unequivocally that the diameter of the lumina consistently diminishes from the central region toward the poles, he wrote only "... lumen of reticulum variable in size." Therefore it became necessary the emendation of the diagnosis of the genus, by which the species having more or less identically sized lumina all over the surface of the pollen will be excluded. This insufficiency of the genusdiagnosis could be the reason that some authors arrange in this genus types which differ from the type species of *Liliacidites*, as SINGH (1971) BRENNER's *P. peroreticulatus* and *P. reticulatus*, or LAING (1975) *Clavatipollenites* and *Retimonocolpites* species while others arrange pollen grains showing the characters of *Liliacidites* not in the reticulate but in the microfoveolate *Arecipites* WODEHOUSE, e.g. ANDERSON (1960) and KRUTZSCH ((1970). Even COUPER (1960) put in *Liliacidites* pollen grains which have a reticulum with lumina of identical size.

Liliacidites hungaricus sp. nov.
(Plate VI., Figs. 1—4)

Derivatio nominis: denominated after the occurrence in Hungary.
Locus typicus: Pénzesgyőr, Mts Bakony, Borehole Pgy-4.
Stratum typicum: 69.7 m. Grey glauconite marl. Pénzeskút Marl Fm., substuderizone, Upper Albian.
Holotype: Slide: Pgy-4., 69.7/2, coord. 31.7—117.9. Pl. VI., Figs. 1—4.

Diagnosis: In distal-polar view boat-shaped, elliptic, medium-sized, thin-walled, semitectate-reticulate, monosulcate pollen. The sulcus reaches from pole to pole, it is a simple slit opening widely at the central part and ending tapered in the polar

regions. The exine is thin, 1.8—2.0 μm. It consists of a smooth, unstructured, 0.8—1.0 μm thick nexine and a structured 1.0—1.2 μm thick sexine. The infratectum of the sexine is formed by 0.5—1.2 μm high bacula standing nearer to each other on the polar parts than in the centre. The tectum is formed by muri connecting the outer ends of the bacula with an irregular reticulum. Width of the muri is about 0.2—0.3 μm the diameter of the lumina is 2—3 μm at the central part and 1.0—1.5 μm in the polar regions.
Dimensions: PD: 36 μm, ED: 24 μm, PD:ED=1.5, PD:et=18—20, st:nt=1.2—1.25.

Differential diagnosis: The new species is similar to *Liliacidites inaequalis* SINGH 1971 but easily be differentiated from it by the smaller size of the lumina, by the more delicate reticulum and by thinner muri.
Occurrence: It has only be observed in the stratum typicum.

Liliacidites simplex sp. nov.
(Plate VI., Figs. 5—9)

Derivatio nominis: it refers to the simple structure.
Locus typicus: Vértessomló (Mts Vértes), Borehole Vst-5.
Stratum typicum: 72.0—73.0 m. Aleurolite. Vértessomló Fm., mamillatum-zone, Lower Albian.
Holotype: Slide: Vst-5, 73.2/2., coord. 37.2—111.1., Pl. VI., Figs. 5—9.

Diagnosis: In polar view boat-shaped, oblong, medium-sized, thin-walled, semitectate-reticulate, monosulcate pollen. The sulcus is a very simple, thin slit reaching from pole to pole. Exine is thin, 1.0—1.5 μm, nexine smooth. The infratectum consists of 0.3—0.4 μm high bacula connected by irregularly shaped muri forming a reticulum with narrow lumina. On some places the reticulum is imperfect.
Dimensions: PD: 29 μm, ED: 18 μm, PD:ED=1.5, PD:et=26—28, st:nt=1.

Differential diagnosis: *Liliacidites simplex* sp. nov. differs from the other *Liliacidites* species by its smaller size, by simpler slit-like sulcus, by the often imperfect reticulum with the smaller lumina which, however, similarly to that of the other *Liliacidites* species further diminishes towards the poles.
Occurrence: This species is one of the most ancient angiospermous pollen grains from Hungarian Albian sediments. Vértessomló Aleurolite Formation, mamillatum-zone, Lower Albian.

Genus: **Trichotomosulcites** COUPER 1953 emend.

Type species: *Trichotomosulcites subgranulatus* COUPER 1953.

Emended diagnosis: Small and medium-sized, relatively thin-walled tectate-columellate, non-reticulate, trichotomosulcate pollen. Amb spheroidal. The nexine unsculptured, the sexine is sculptured by granulate, verrucate and microfoveolate elements. The three-armed sulcus is wide, reaching to the equator; often ornamented with granula, verrucae.

Differential diagnosis: This genus separated from other trichotomosulcate, thin-walled genera by it non-reticulate (granulate, verrucate, microfoveolate) ornamentation.

Trichotomosulcites maior sp. nov.
(Plate VI., Figs. 10—12)

Locus typicus: Olaszfalu (Mts Bakony). Borehole Ot-84.
Stratum typicum: 16.0 m. Clayey-marl. Tés Clay Fm. Middle Albian.
Holotype: Slide: Ot-84, 16/2., coord. 34.1—104.2. Pl. V., Figs. 10—12.

Diagnosis: Rounded-triangular, trichotomosulcate pollen. The sulcus forms a triangular arch reaching nearly to equator. Exine is 2 μm thick, the ratio sexine: nexine = 1, they are scarcely differentiated. The area of three-armed sulcus is ornamented by granula, the other part of pollen grain is microfoveolate.
Height of granula: 0.3—0.5 μm, size of microfoveolae: height: 0.6—0.8 μm, width: 0.2—0.3 μm.
Dimensions: PD: 40—42 μm, ED: 39—41 μm, length of the sulcus: 22—24 μm, its thickness is 1.5 μm.

Differential diagnosis: The new species differs from *Trichotomosulcites subgranulatus* COUPER 1953, *Trichotomosulcites waronuiensis* COUPER 1953 and *Trichotomosulcites contractus* ANDERSON 1960 by its larger size, thicker exine and by particularly granulate, mostly microfoveolate ornamentation. The other trichotomosulcate species (from genera *Oroszlanyipollis* GÓCZÁN et JUHÁSZ 1984, *Singhipollis* gen. nov.) are reticulate form.
Occurrence: Pénzeskút Marl Formation, Upper Albian.

Genus: **Foveomonocolpites** gen. nov.

Type species: *Foveomonocolpites pereensis* gen. nov. et sp. nov.

Genusdiagnosis: Monosulcate angiosperm pollen grains with strongly elongated, boat-shaped contour and narrow sulcus. The exine is tectate-perforate, moderately thick. The ratio of sexine: nexine = 1. The sexine has a microfoveolate-microfoveoreticulate ornamentation.

Differential diagnosis: *Foveomonocolpites* gen. nov. differs from the other monosulcate, thin-walled early angiospermous pollen genera by its non-reticulate, microfoveolate sculpture and by its elongated, boat-shaped, "magnoliid-type" form. The *Arecipites* WODEHOUSE 1933 is also microfoveolate (scrobiculate) but a form of the Palmae-type. *Foveomorphomonocolpites* SOLE de PORTA 1971 differs from the new genus by its less prolate contours and thicker wall.

Foveomonocolpites pereensis gen. nov. et sp. nov.
(Plate VI., Figs. 13—18)

Derivatio nominis: after the village Pere, Bakony Mts. (Hungary).
Locus typicus: Pere, Borehole Pe-27.
Stratum typicum: 126.0 m, grey-marl, Pénzeskút Fm., Lower Cenomanian.
Holotype: Slide: Pe-27, 126/2., coord. 35.2—108.4. Pl. VI., Figs. 13—18.

Diagnosis: Very elongated, boat-shaped, large-sized, monosulcate pollen. The sulcus reaches from pole to pole, it is thin, hardly opened. Exine is about 1 μm thick and perforated by microfoveolae of 0.5 μm in diameter. The microfoveolae are densely spaced and therefore the sculpture of the pollen has a microfoveolate-microreticulate character.
Dimensions: PD: 77 μm, ED: 29 μm, PD:ED = 2.1—2.5, length of sulcus: 65 μm.

Differential diagnosis: The new species differs from the monosulcate angiospermous pollen grains described until now from the Barremian up to the Cenomanian by its peculiar sculpture, with its very large size and its characteristic form similar to that of the recent magnoliid pollen grains.

Occurrence: Up till now it was observed only in sediments of mantelli-zone of Pénzeskút Marl Formation (Lower Cenomanian).

A new system of the early monosulcate-trichotomosulcate angiosperm pollen grains

Turma: **Archaeangiospermae** nov. turma
(Mono- et trichotomosulcate primarum Angiospermarum)

1. Subturma: *Crassinexines* nov. subturma
1.1. Infraturma: *Crassinexines-Reticulati* nov. infraturma
1.1.1. Subinfraturma: *Crassinexines-Retimonosulcati* nov. subinfraturma
1.1.1.1. Forma Genus: *Similipollis* GÓCZÁN et JUHÁSZ 1984
1.1.1.1.1. Forma Species: *Similipollis varireticulatus* GÓCZÁN et JUHÁSZ 1984
1.1.1.1.2. Forma Species: *S. orbiculatus* GÓCZÁN et JUHÁSZ 1985
1.1.1.2. Forma Genus: *Harskutipollis* nov. genus
1.1.1.2.1. Forma Species: *Harskutipollis robustus* nov. sp.
1.1.2. Subinfraturma: *Crassinexines-Reticulotrichotomosulcati* nov. subinfraturma
1.1.2.1. Forma Genus: *Oroszlanyipollsi* GÓCZÁN et JUHÁSZ 1984
1.1.2.1.1. Forma Species: *Oroszlanyipollis grandis* GÓCZÁN et JUHÁSZ 1984
1.1.2.1.2. Forma Species: *Oroszlanyipollis baconicus* GÓCZÁN et JUHÁSZ 1985
1.1.2.1.3. Forma Species: *O. saparensis* GÓCZÁN et JUHÁSZ 1985
1.2. Infraturma: *Crassinexines-Nonreticulati* nov. infraturma
1.2.1. Subinfraturma: *Crassinexines-Nonreticulomonosulcati* nov. subinfraturma
1.2.1.1. Forma Genus: *Crassipollis* GÓCZÁN et JUHÁSZ 1984
1.2.1.1.1. Forma Species: *Crassipollis pusztavamensis* GÓCZÁN et JUHÁSZ 1984
1.2.1.1.2. Forma Species: *Cr. deakae* GÓCZÁN et JUHÁSZ 1984
1.2.1.1.3. Forma Species: *Cr. vraconicus* GÓCZÁN et JUHÁSZ 1984
1.2.1.1.4. Forma Species: *Cr. ovalis* GÓCZÁN et JUHÁSZ 1984
1.2.1.1.5. Forma Species: *Cr. vertesensis* GÓCZÁN et JUHÁSZ 1984
1.2.1.1.6. Forma Species: *Cr. dissimilis* GÓCZÁN et JUHÁSZ 1984
1.2.1.1.7. Forma Species: *Cr. minor* GÓCZÁN et JUHÁSZ 1984
1.2.1.1.8. Froma Species: *Cr. urkutensis* GÓCZÁN et JUHÁSZ 1985
1.2.1.1.9. Forma Species: *Cr. noszkyii* GÓCZÁN et JUHÁSZ 1985
1.2.1.1.10. Forma Species: *Cr. magnus* GÓCZÁN et JUHÁSZ 1985
1.2.1.1.11. Forma Species: *Cr. minimus* GÓCZÁN et JUHÁSZ 1985
1.2.1.1.12. Forma Species: *Cr. pyriformis* GÓCZÁN et JUHÁSZ 1985
1.2.1.1.13. Forma Species: *Cr. longisulcatus* GÓCZÁN et JUHÁSZ 1985
1.2.1.1.14. Forma Species: *Cr. tesensis* GÓCZÁN et JUHÁSZ 1985
2. Subturma: *Tenuinexines* nov. subturma
2.1. Infraturma: *Tenuinexines-Reticulati* nov. infraturma
2.1.1. Subinfraturma: *Tenuinexines-Reticulomonosulcati* nov. subinfraturma

2.1.1.1. Forma Genus: *Brenneripollis* nov. gen.
2.1.1.1.1. Forma Species: *Brenneripollis pellitus* nov. sp.
2.1.1.1.2. Forma Species: *Br. gracilis* nov. sp.
2.1.1.1.3. Forma Species: *Br. surensis* nov. sp.
2.1.1.1.4. Forma Species: *Br. peroreticulatus* (BRENNER 1963) comb. nov.
2.1.1.1.5. Forma Species: *Br. reticulatus* (BRENNER 1963) comb. nov.
2.1.1.1.6. Forma Species: *Brenneripollis textus* (NORRIS 1967) comb. nov.
2.1.1.1.7. Forma Species: *Br. crassatus* (SINGH 1971) comb. nov.
2.1.1.2. Forma Genus: *Retimonocolpites* PIERCE 1961. emend.
2.1.1.2.1. Forma Species: *Retimonocolpites dividuus* PIERCE 1961
2.1.1.2.2. Forma Species: *R. rotundus* (KEMP 1968) comb. nov.
2.1.1.2.3. Forma Species: *R. fragilis* PIERCE 1961
2.1.1.3. Forma Genus: *Liliacidites* COUPER 1953 emend.
2.1.1.3.1. Forma Species: *Liliacidites kaitangataensis* COUPER 1953
2.1.1.3.2. Forma Species: *L. variegatus* COUPER 1953
2.1.1.3.3. Forma Species: *L. intermedius* COUPER 1953
2.1.1.3.4. Forma Species: *L. giganteus* SINGH 1983
2.1.1.3.5. Forma Species: *L. magnus* SINGH 1983
2.1.1.3.6. Forma Species: *L. lenticularis* SINGH 1983
2.1.1.3.7. Forma Species: *L. dictyotus* SINGH 1983
2.1.1.3.8. Forma Species: *L. tectatus* SINGH 1983
2.1.1.3.9. Forma Species: *L. hungaricus* nov. sp.
2.1.1.3.10. Forma Species: *L. simplex* nov. sp.
2.1.1.4. Forma Genus: *Clavatipollenites* COUPER 1958
2.1.1.4.1. Forma Species: *Clavatipollenites hughesii* COUPER 1958
2.1.1.4.2. Forma Species: *Cl. minutus* BRENNER 1963
2.1.1.4.3. Forma Species: *Cl. tenellis* PHILLIPS et FELIX 1971
2.1.1.4.4. Forma Species: *Cl. clavatus* (SINGH 1971) comb. nov.
2.1.1.4.5. Forma Species: *Cl. incisus* CHLONOVA 1977
2.1.1.5. Forma Genus: *Stellatopollis* DOYLE 1975
2.1.1.5.1. Forma Species: *Stellatopollis barghoornii* DOYLE 1975
2.1.1.5.2. Forma Species: *Stellatopollis largissimus* SINGH 1983
2.1.2. Subinfraturma: *Tenuinexines-Reticulotrichotomosulcati* nov. subinfraturma
2.1.2.1. Forma Genus: *Singhipollis* nov. gen.
2.1.2.1.1. Forma Species: *Singhipollis microreticulatus* nov. sp.
2.1.2.1.2. Forma Species: *Singhipollis vulgaris* (GROOT et GROOT 1962) comb. nov.
2.1.2.1.3. Forma Species: *Singhipollis trichotomosulcatus* (SINGH 1971) comb. nov.
2.1.2.1.4. Forma Species: *Singhipollis orbiculatus* (SINGH 1971) comb. nov.
2.2. Infraturma: *Tenuinexines-Nonreticulati* nov. infraturma
2.2.1. Subinfraturma: *Tenuinexines-Nonreticulomonosulcati* nov. subinfraturma
2.2.1.1. Forma Genus: *Transitoripollis* GÓCZÁN et JUHÁSZ 1984
2.2.1.1.1. Forma Species: *Transitoripollis anulisulcatus* GÓCZÁN et JUHÁSZ 1984
2.2.1.1.2. Forma Species: *Tr. similis* GÓCZÁN et JUHÁSZ 1984
2.2.1.1.3. Forma Species: *Tr. praesimilis* GÓCZÁN et JUHÁSZ 1984
2.2.1.1.4. Forma Species: *Tr. vulgaris* GÓCZÁN et JUHÁSZ 1985
2.2.1.1.5. Forma Species: *Tr. ovalis* GÓCZÁN et JUHÁSZ 1985

2.2.2. Subinfraturma: *Tenuinexines-Nonreticulotrichotomonosulcati* nov. subinfraturma
2.2.2.1. Forma Genus: *Trichotomosulcites* COUPER 1953 emend.
2.2.2.1.1. Forma Species: *Trichotomosulcites subgranulatus* COUPER 1953
2.2.2.1.2. Forma Species: *Trichotomosulcites contractus* ANDERSON 1960
2.2.2.1.3. Forma Species: *Trichotomosulcites maior* nov. sp.
2.3. Infraturma: *Tenuinexines-Foveolati* nov. infraturma
2.3.1. Subintrafturma: *Tenuinexines-Foveomonosulcati* nov. subinfraturma
2.3.1.1. Forma Genus: *Foveomonocolpites* nov. gen.
2.3.1.1.1. Forma Species: *Foveomonocolpites pereensis* nov. sp.
2.3.1.2. Forma Genus: *Arecipites* WODEHOUSE 1933
2.3.1.2.1. Forma Species: *Arecipites punctatus* WODEHOUSE 1933

Plate I.

1—20 *Brenneripollis pellitus* nov. gen. et nov. sp. (genotype)
Súr, Bore Súr-1., 535.6—538.5 m, "munieria" marl. Tés Clay Formation, Middle Albian.
Slide: 535/2, coord.: 5.5—94.8. Figs. 1—15=1000×, 16—18=2000×, 19—20=3000×.
21—31 *Brenneripollis gracilis* nov. sp. (holotype)
Tés, Bore Tt-27., 38.5 m. Tés Clay Formation, Middle Albian
Slide: 38.5/2, coord.: 4.3—105.5.
32—42 *Brenneripollis gracilis* nov. sp. (paratype)
Súr, Bore Súr-1., 526.8—529 m. Tés Clay Formation.
Slide: 526/1., coord.: 6.5—100.7.

Plate II.

1—10 *Brenneripollis peroreticulatus* (BRENNER 1963) nov. comb.
Olaszfalu, Bore Pe-31., 127.0—128.0 m. Pénzeskút Marl Formation, bergeri-subzone. Upper Albian. Slide: 127/1., coord.: 19.7—105.5.
11—15 *Brenneripollis peroreticulatus* (BRENNER 1963) nov. comb.
Úrkút, Bore U-421., 341.2 m. Upper part of Tés Clay Fm.
Slide: 341.2/1., coord.: 32.9—102.4.
16—20 *Brenneripollis reticulatus* (BRENNER 1963) nov. comb.
Balinka, Bore Ba-288., 602.0 m. Tés Clay Fm. Middle Albian.
Slide: 602/1., coord.: 15.8—100.4.
21—25 *Brenneripollis reticulatus* (BRENNER 1963) nov. comb.
Balinka, Bore Ba-288., 602.0 m. Tés Clay Fm. Middle Albian.
Slide: 602/1., coord.: 9.9—104.2.
26 *Brenneripollis reticulatus* (BRENNER 1963) nov. comb.
Pénzesgyőr, Bore Pgy-4., 69.7. Pénzeskút Marl Fm., inflatum-zone, Upper Albian.
Slide: 69.7/1. coord.: 36.5—95.0.
27—30 *Brenneripollis reticulatus* (BRENNER 1963) óov. comb.
Olaszfalu, Bore Ot-84., 80.0 m, Tés Clay Fm. Middle Albian.
Slide: 80/1., coord.: 39.7—111.5.

Plate III.

1—7 *Brenneripollis tectus* (NORRIS 1967) nov. comb.
Vértessomló. Bore Vst-5., 50.0—51.5 m. Vértessomló Aleurolite Formation,mammilatum-zone, Lower Albian.
Slide: 50/1., coord.: 7.4—105.6.
8—15 *Brenneripollis tectus* (Norris 1967) nov. comb.
Súr, Bore Súr-1., 545.8—547.1 m. Tés Clay Fm. Middle Albian.
Slide: 545/1., coord.: 15.5—93.7.
16—25 *Brenneripollis tectus* (NORRIS 1967) nov. comb.
Súr, Bore Súr-1., 533.0—533.6 m. Tés Clay Fm. Middle Albian.
Slide: 533/1., coord.: 6.3—93.6.

26—35 *Brenneripollis tectus* (NORRIS 1967) nov. comb.
Vértessomló, Bore Vst-4., 181.0 m. Vértessomló Aleurolite Fm., mammilatum-zone, Lower Albian.
Slide: 181/1., coord.: 14.8—93.8.

Plate IV.

1—12 *Brenneripollis surensis* nov. sp. (holotype)
Súr, Bore Súr-1., 538.8 m. Tés Clay Fm. Middle Albian.
Slide: 538.8/3., coord.: 36.0—96.8.
13—17 *Retimonocolpites rotundus* (KEMP 1968) nov. comb.
Súr, Bore Súr-1., 553.6 m. Tés Clay Fm. Middle Albian.
Slide: 553/1., coord.: 18.5—101.0.
18—25 *Harskutipollis robustus* nov. sp. (holotype)
Hárskút, Bore Hk-4., 133.0—135.1 m. Pénzeskút Marl Fm., dispar-zone, Upper Albian.
Slide: 69—70/2., coord.: 16.8—108.6.
26—29 *Harskutipollis robustus* nov. sp. (paratype)
Hárskút, Bore Hk-4., 127.0 m. Pénzeskút Marl Fm., dispar-zone, Upper Albian.
Slide: 19/4., coord.: 8.0—104.

Plate V.

1—5 *Clavatipollenites hughesii* COUPER 1958
Tés, Bore Tt-27., 49.0 m. Tés Clay Fm. Middle Albian.
Slide: 49/2., coord.: 20.4—102.8.
6—10 *Clavatipollenites hughesii* COUPER 1958
Úrkút, Bore U-4., 44.0—45.0 m. Pénzeskút Marl Fm., bergeri-subzone. Upper Albian.
Slide: U/2-2., coord.: 7.3—117.8.
11—12 *Clavatipollenites minutus* BRENNER 1963
Vértessomló, Bore Vst-5., 44.5 m. Vértessomló Aleurolite Fm., mammilatum-zone Lower. Albian.
Slide: 44.5/1, coord.: 7.1—92.
13 *Clavatipollenites minutus* BRENNER 1963
Olaszfalu, Bore Ot-83., 30.0 m. Tés Clay Fm. Middle Albian.
Slide: 30/3., coord.: 32.1—100.2.
14 *Clavatipollenites* cf. *minutus*
Pénzesgyőr, Bore Pgy-4., 69.7 m. Pénzeskút Marl Fm., bergeri subzone, Upper Albian.
Slide: 69.7/9, coord.: 7.2—94.1.
15 *Clavatipollenites tenellis* PHILLIPS et FELIX 1971
Csehbánya, Bore Cseh-13., 263.0 m. Tés Clay Fm. Middle Albian.
Slide: 263/3., coord. 12.1—110.6.
16—19 *Clavatipollenites tenellis* PHILLIPS et FELIX 1971
Tés, Bore Tt-27., 49.0 m. Tés Clay Fm. Middle Albian.
Slide: 49/2., coord.: 14.4—103.3.
20—24 *Clavatipollenites tenellis* PHILLIPS et FELIX 1971
Vértessomló, Bore Vst-4. 87.0 m. Vértessomló Aleurolite Fm., mammilatum-zone, Lower Albian.
Slid e: 87/3., coord.: 19.0—94.3.
25—30 *Singhipollis microreticulatus* nov. gen. et nov. sp. (holotype)
Tés, Bore Tt-27., 49.0 m. Tés Clay Fm. Middle Albian.
Slide: 49/2., coord.: 15.3—105.0.

Plate VI.

104 *Liliacidites hungaricus* nov. sp. (holotype)
Pénzesgyőr, Bore Pgy-4., 69.7 m. Pénzeskút Marl Fm., substuderi-zone. Upper Albian.
Slide: 69.7/2., coord.: 31.7—117.9.
5 *Liliacidites simplex* nov. sp. (holotype)
Vértessomló, Bore Vst-5., 72.0—73.2 m. Vértessomló Aleurolite Fm., mammilatum-zone. Lower Albian.
Slide: 73.2/2., coord.: 37.2—111.1.
10—12 *Trichotomosulcites maior* nov. sp. (holotype)
Olaszfalu, Bore Ot-84., 16.0 m. Tés Clay Fm. Middle Albian.
Slide: 16/2., coord.: 34.1—104.2.
13—16 *Foveomonocolpites pereensis* nov. sp. (holotype)
Olaszfalu, Bore Pe-27., 56.7 m. Pénzeskút Marl Fm., mantelli-zone. Lower Cenomanian.

Plate I

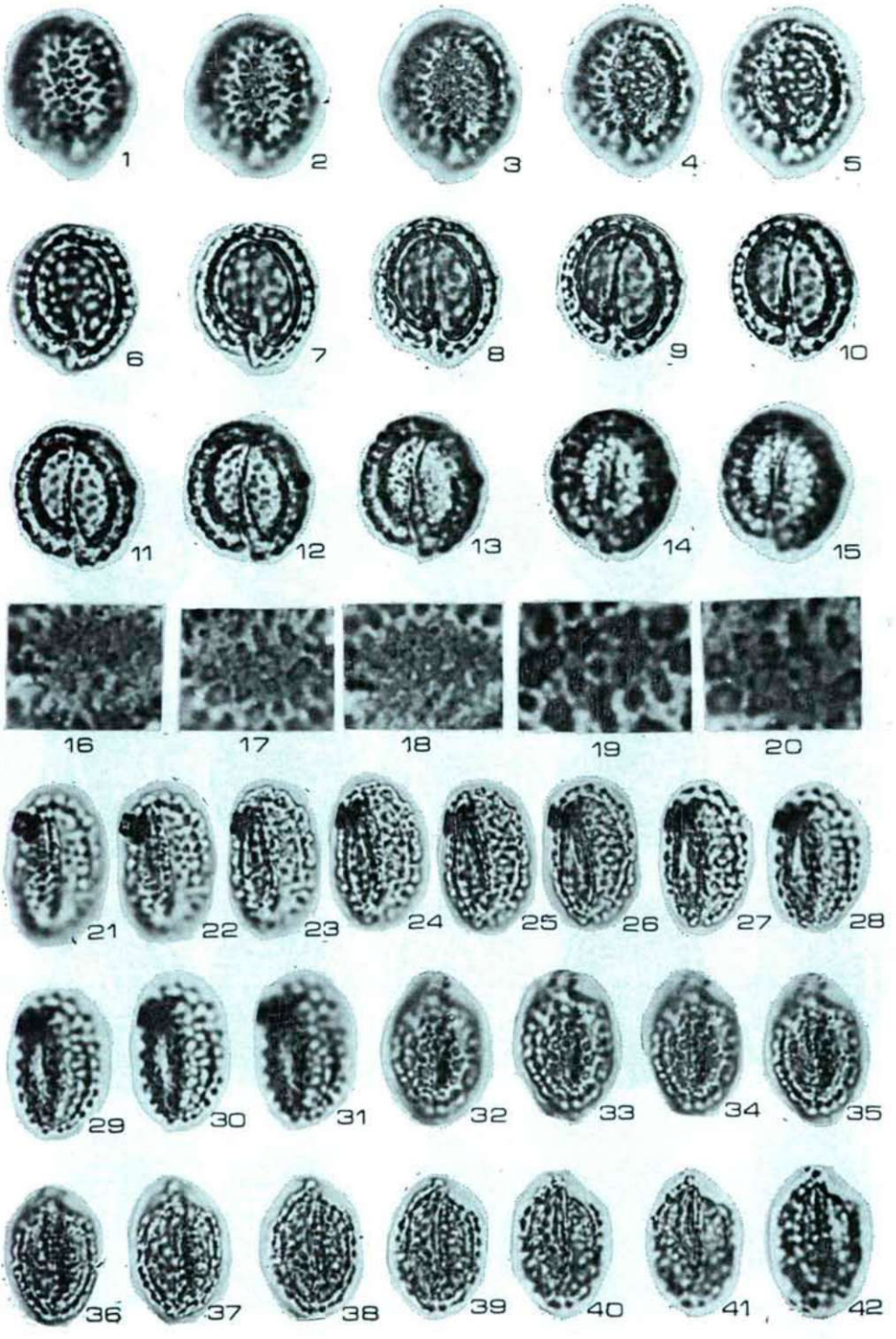
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Plate II

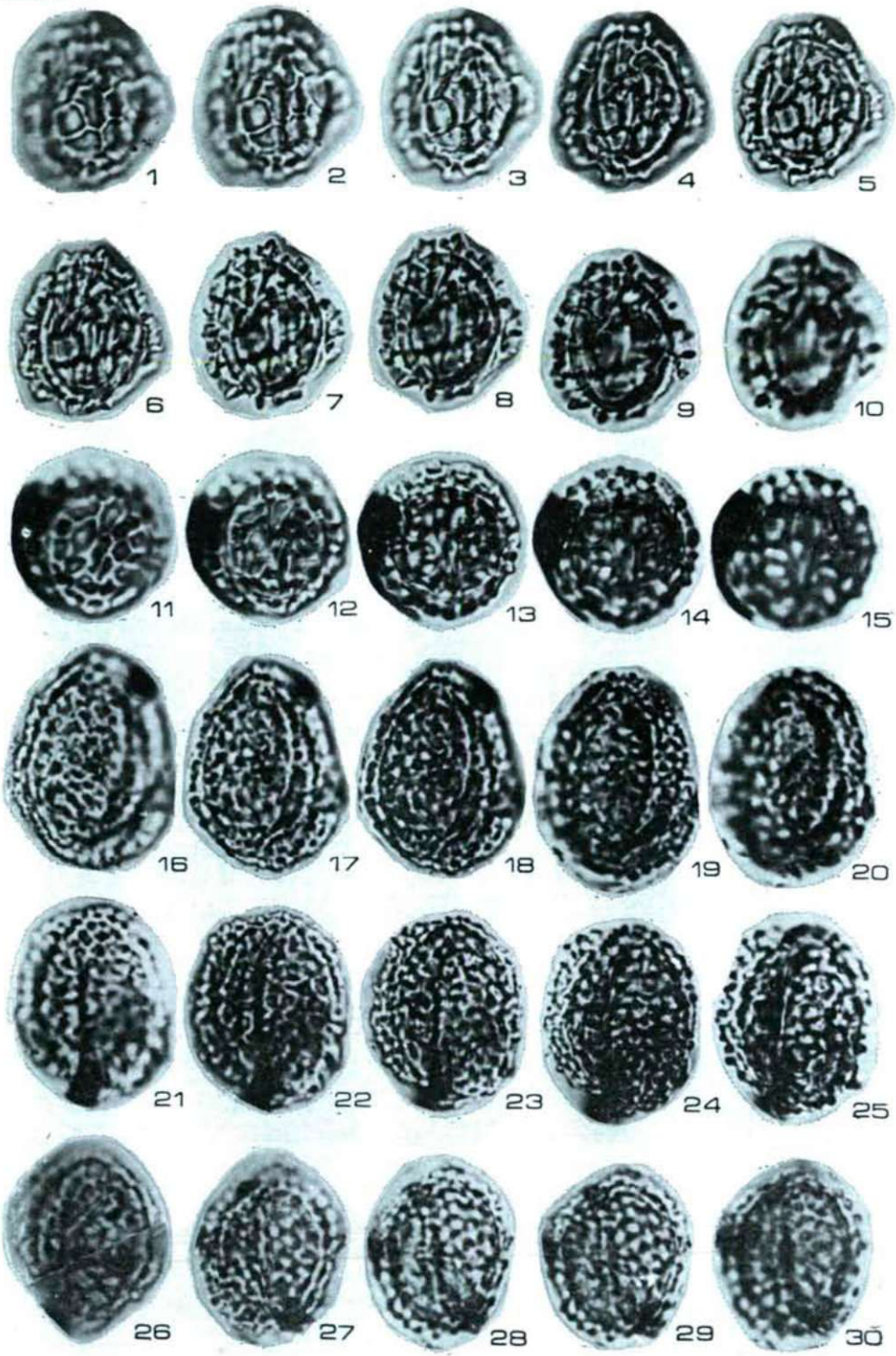
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Plate III

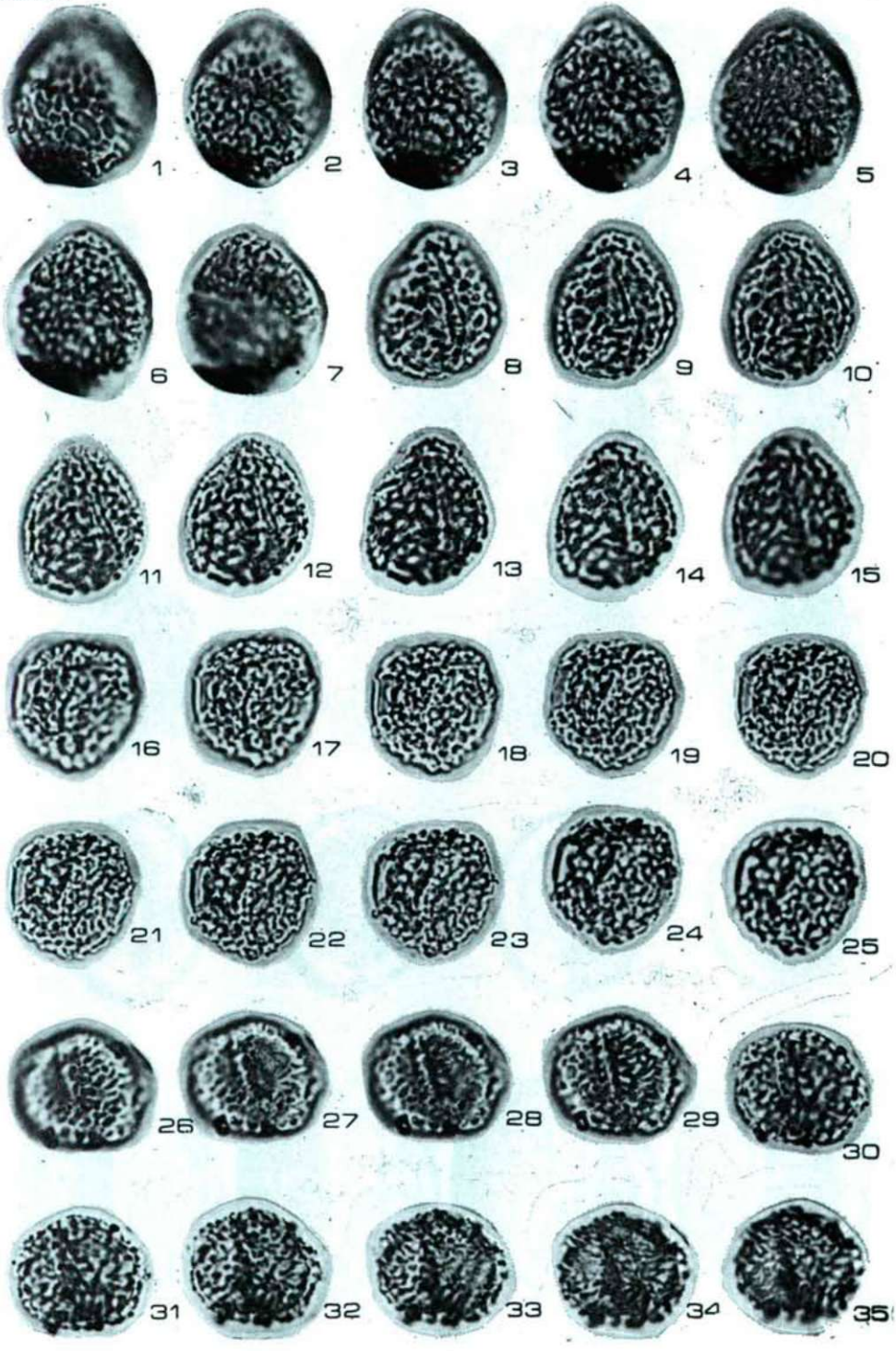
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Plate IV

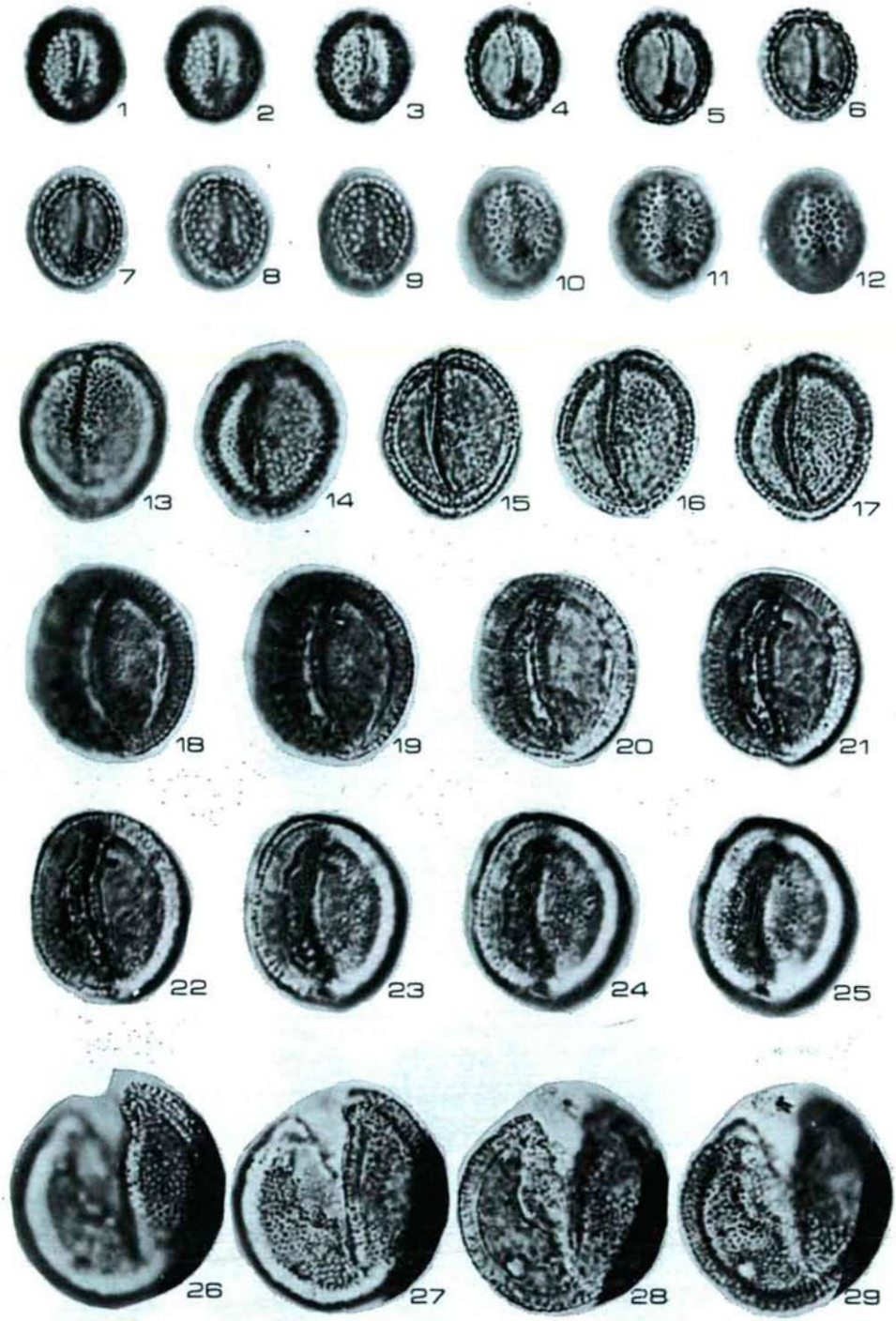

Plate V

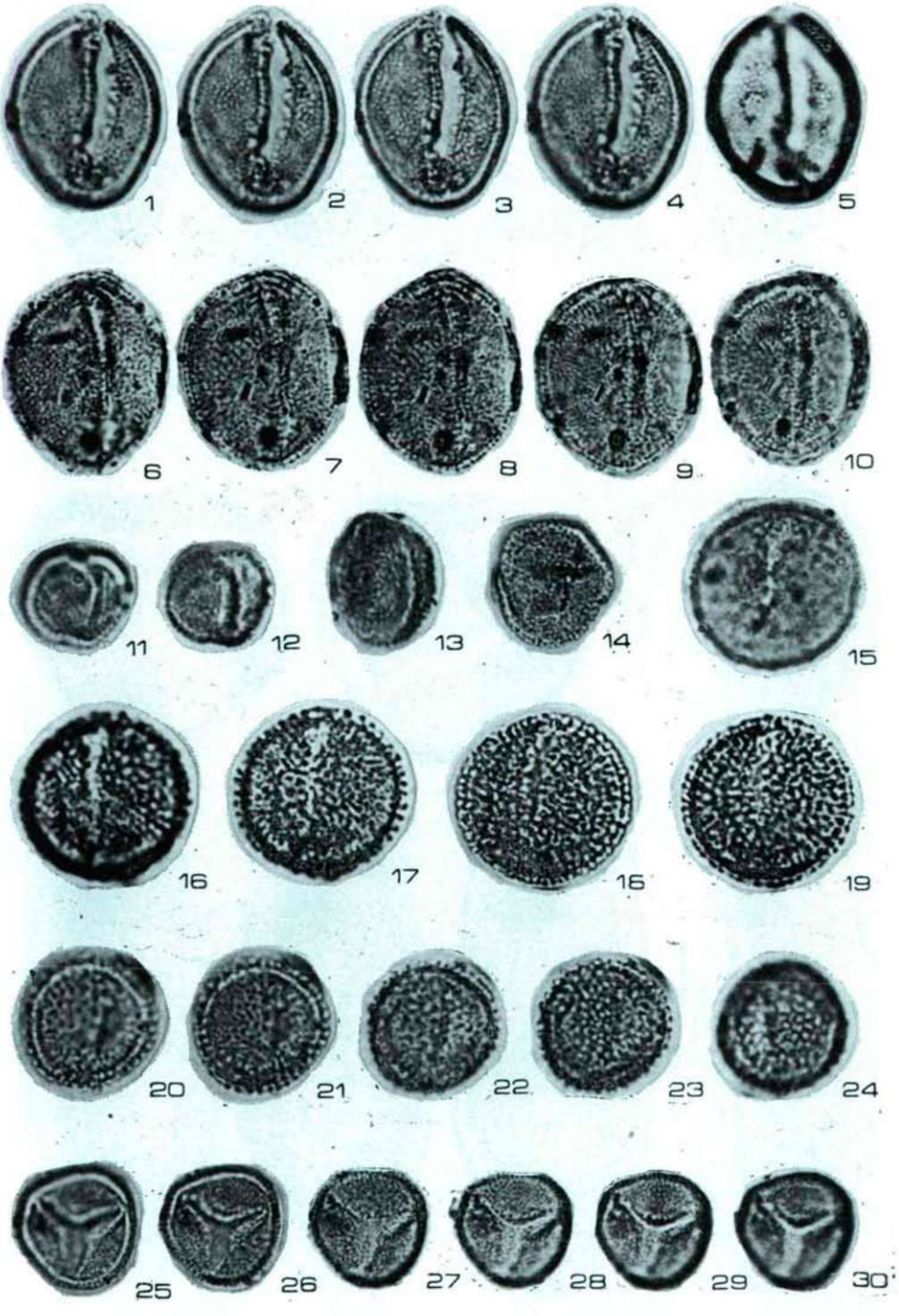
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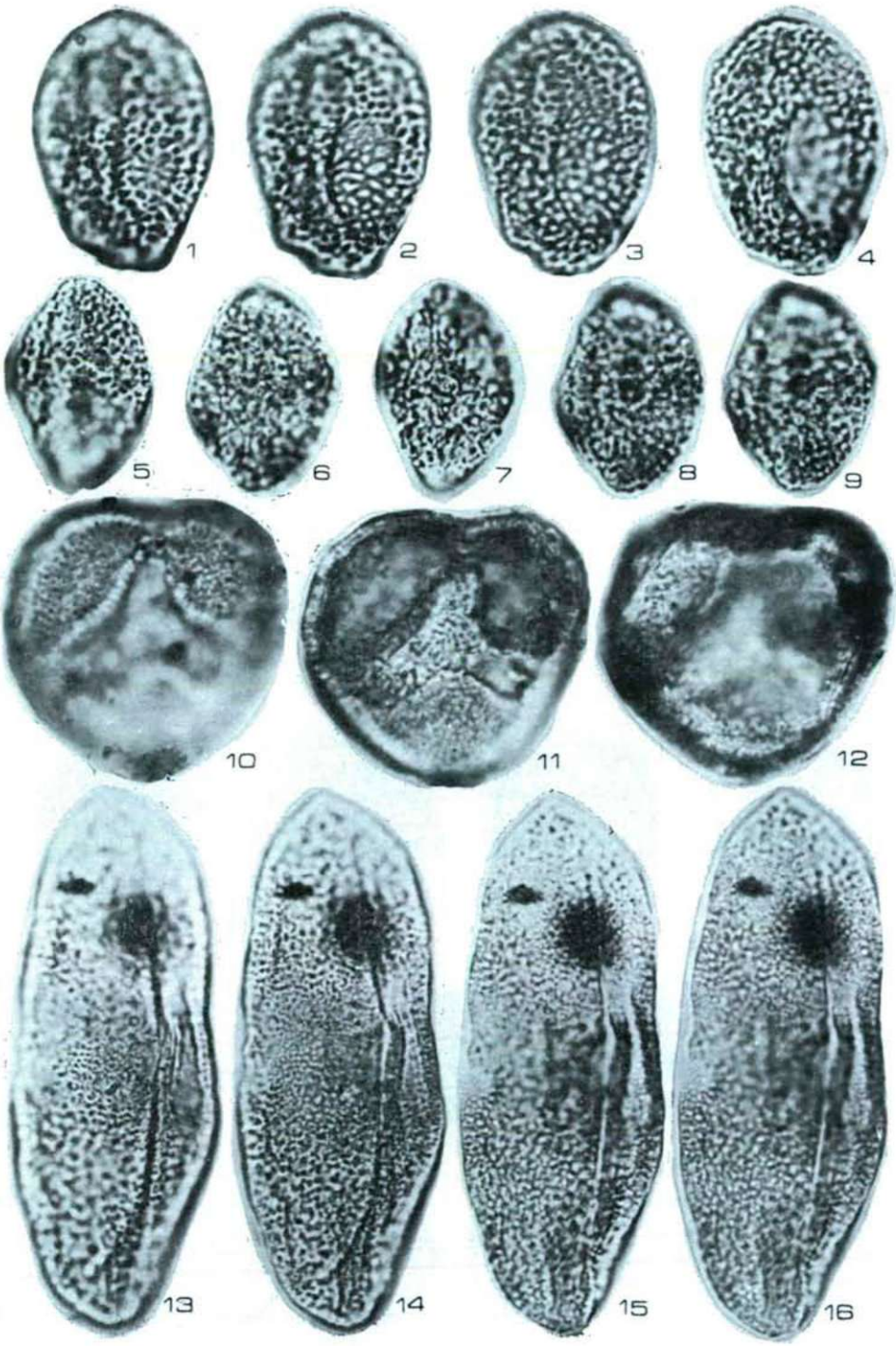
Plate VI



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DETERMINATION OF THE DEGREE OF INTRASPECIFIC COMPETITION IN MONOCULTURES

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Abstract

The maximal distance of interference between individuals of plant populations of the same age can be determined by measuring the dry mass of the plant individuals and the distance between the surrounding individuals. The degree of competition is proportional to the number of the neighbouring individuals and the square of their distance. In lack of competition the maximal mass of the plant individuals of given age can be calculated from the reckoned degree of the competition as well as from the measured dry masses. That distance grade approaches the maximal distance of the competitive effect, where the maximal dry mass is of the highest value.

Key words: density dependence, distance of interference, neighbourhood model, *Plantago indica, Scabiosa ochroleuca.*

Introduction

In the various plant populations the organic matter production of the average plant individual is in regular relationship with the density of the neighbouring individuals in the environs.

The average dry mass of individuals of populations grown in monoculture gives a horizontal and a sloping straight line, respectively, in the function of the density of the individuals illustrated on logarithmic scale. The intersection of these lines is found at that critical density where the individuals of given age are already in competitive interaction (KIRA et al., 1953). The difficulty of the method is that two linear regressions have to be applied at the same time. SHINOZAKI et al. (1956) established linear connection between the reciprocal of mean plant weight and the density ("reciprocal yield law"). Apart from density, the distance of the neighbouring individuals can also be used for expressing the competitive effect (MACK and HARPER, 1977; WEINER, 1982). WEINER (1982) suggested the neighbourhood model for determining the degree of interactions, where he counted the number of the neighbouring individuals around the testindividual in concentric rings and the degree of competition was proportionated to the square of the median distance of the rings (neighbourhoods).

In this paper the aim was to seek for a suitable method, setting out from the previous model, which could be used in the case of a small number of samples for determining the distance where the individuals start to influence each others growth in a population of given age.

THE MODEL

Such function is suitable for the description of the result of density-dependent competition, which has maximal values if there is no competition, and asymptotically nears to zero with the increase in density. One of the simplest functions of this kind is the hyperbola, which was applied by KIRA et al. (1953) for the production of evenly distributed population in the reciprocal yield law. The mathematic description of this is as follows:

$$\frac{1}{V} = a + bN \tag{1}$$

where V=average plant production
N=density of the population.
This model was elaborated by WEINER (1982) in his neighbourhood-model as follows:

$$\frac{1}{V} = \frac{1 + W}{V_{max}} \tag{2}$$

where W=the degree of competition, furthermore

$$W = \sum_{i=1}^{n} \frac{1}{d_i^2} \sum_j C_j N_{ij} \tag{3}$$

where d_i = the average distance of the ith neighbourhood,

N_{ij} = the individual count of the jth species in the ith neighbourhood,
C_j = average competitive effect of an individual from the jth species.

The farthest neighbourhood ($i=n$) is regarded where the individuals are still in interaction with the test individual.

When studying the monoculture of a species the (2) formula could be set down in the following form:

$$\frac{1}{V} = \frac{1 + C \Sigma \frac{N_i}{d_i^2}}{V_{max}}. \tag{4}$$

The neighbourhood-model composed of concentric rings could rather be applied to populations of nonuniform distribution (WEINER, 1982). In uniformly distributed population the median distance of the concentric rings could be substituted for the concrete distance of the neighbouring individuals, in such way the under- or overestimation of the degree of competition becomes exterminable which occurs in the case of the unequality of the two distances.

In this paper the slightly modified variant of the model described above was used for determining the degree of competition and the distance of interaction regarding plant individuals of uniformly distributed *Plantago indica* and *Scabiosa ochroleuca* populations, grown in laboratory.

The concrete distance of each individual was used instead of the median distance of the concentric rings. In the case of hexagonal regular pattern the neighbouring

individuals are arranged along the concentric rings (which is analogous to the median distance of the "neighbourhood").

The relative distance and the individual count of the neighbouring individuals in the populations of hexagonal arrangement are demonstrated in Tables 1 and 3. The measured distance of the neighbouring individuals in the population of various density is also shown in these Tables.

Materials and Methods

The annual xerophyton *Plantago indica* L. and the perennial *Scabiosa ochroleuca* L. are the members of the secondary succession of the experimental grasslands at Bugacpuszta. Knowledge on the inter- and intraspecific interactions complements the population dynamic survey carried out at the area.

The studied populations of the two plant species were grown in light chambers under controlled conditions at 20—25 °C temperature besides 8000 Lux light intensity, in 10/14 hr light-dark cycle. Seeds collected from the experimental area at Bugacpuszta were used for sowing and the sandy soil of the experimental area was used as substrate. (For characteristic parameters of soil see: KÖRMÖCZI, 1983).

The sowing was prepared in 30×30×10 cm sized plastic boxes in 4 different densities in regular hexagonal arrangement. The average densities and the average distance of the neighbouring individuals were: 10.4, 18.5, 25.2, 37.3 individual/dm² and 3.3, 2.5, 2.1, and 1.8 cm resp., in the case of *Plantago indica,* and 5.7, 9.4, 18.5, 51.3 individual/dm² and 4.5, 3.5, 2.5, and 1.5 cm, resp., in the case of *Scabiosa ochroleuca.*

The plants were watered with destilled water by spraying from the top.

The *Plantago* crop was processed at the age of 3 moths. From every stand the part above the soil was cut off in the case of 20—20 individuals and the dry mass and leaf count was calculated.

The *Scabiosa* crop was harvested with the same method at the age of 2.5 months, but in this case the above parameters were measured on 30—50 inqividuals.

Results

By evaluating the expreimental data the aim was to determine the distance (d_{max}) within which interference may occur between the individuals of the studied population. Hence, when calculating the degree of competition (W) the presumed maximal distance of the competition was gradually increased by 0.5 cm. The resulted W-values are demonstrated in Tables 2 and 4, in respect to both dry matter and leaf count.

Table I. Data regarding the distance of the *Plantago* individuals

ith neighbour	N_i	m_{rel}	measured distances at the various densities (cm)			
			10.4	18.5	25.2	37.3
1	6	1.00	3.3	2.5	2.1	1.8
2	6	1.73	5.8	4.3	3.7	3.1
3	6	2.00	6.7	5.0	4.3	3.5
4	12	2.66	8.8	6.6	5.7	4.7
5	6	3.00	10.0	7.5	6.4	5.3
6	6	3.46		8.7	7.4	6.1

N_i = individual number of the *i*th neighbour
m_{rel} = relative distance of the *i*th neighbour, if $m_1 = 1$.

Following this, regression analysis was performed per d_{max}-grade for determining the V_{max} and C values. In the case of both studied variables the measured values corresponded best to that expected if the presumed maximal distance was 4.5 cm in the case of *Plantago indica* population. The best correlation coefficient was 0.96 for the dry matter and 0.98 for the leaf count. The W-values as well as the V_{max}-values of. the studied parameters were also the highest at 4.5 cm distance (Tables 1, 2; Figs. 1, 2).

Table 2. W values in the *Plantago* crops calculated on the basis of individual density and dry matter relatedness.

Nr	d_{max}	W				r	C	V_{max}
		10.4	18.5	25.2	37.3			
1	3.0	0.00	1.08	1.47	2.18	0.90	1.13	88.46
2	3.5	0.67	1.19	1.62	3.20	0.89	1.24	108.16
3	4.0	0.55	0.98	1.77	3.12	0.94	1.02	105.55
4	4.5	0.74	1.75	2.83	4.19	0.96	1.37	139.92
5	5.0	0.48	1.36	1.85	3.23	0.91	0.89	110.61
6	5.5	0.41	1.15	1.57	2.90	0.90	0.76	101.61
7	6.0	0.62	1.31	1.77	3.31	0.90	0.86	111.57

W values in *Plantago* crops calculated on the basis of individual density and leaf number relatedness.

Nr	d_{max}	W				r	C	V_{max}
		10.4	18.5	25.2	37.3			
1	3.0	0.00	0.23	0.31	0.46	0.92	0.24	23.42
2	3.5	0.13	0.23	0.31	0.61	0.93	0.24	24.63
3	4.0	0.10	0.18	0.34	0.59	0.97	0.19	24.38
4	4.5	0.11	0.27	0.43	0.63	0.98	0.21	25.44
5	5.0	0.09	0.25	0.34	0.59	0.95	0.16	24.62
6	5.5	0.08	0.23	0.31	0.57	0.94	0.15	24.26
7	6.0	0.11	0.24	0.33	0.61	0.94	0.16	24.73

In the case of *Scabiosa ochroleuca* the correlation of the regression line in the case of both studied variables (dry mass and leaf number) showed maximum ad $d_{max}=2.5$ cm value (0.98 and 0.90), however, the highest values of V_{max} were obtained in the case when $d_{max}=5.0$ cm (67.6 and 12.2), and even the rise of the regression line was the slightest at this value (Tables 3 and 4; Figs. 3, 4.).

Table 3. Data of distances for *Scabiosa ochroleuca* individuals

ith neighbour	N_i	m_{rel}	measured distances at the various densities (cm)			
			5.7	9.4	18.5	51.3
1	6	1.00	4.5	3.5	2.5	1.5
2	6	1.73	7.8	6.1	4.3	2.6
3	6	2.00	9.0	7.0	5.0	3.0
4	12	2.66	12.0	9.3	6.7	4.0
5	6	3.00	13.5	10.5	7.5	4.5
6	6	3.46	15.6	12.1	8.6	5.2
7	12	3.61	16.3	12.6	9.0	5.4

Table 4. W values in *Scabiosa* crops calculated on the basis of individual density and dry matter relatedness

Nr	d_{max}	W				r	C	V_{max}
		5.7	9.4	18.5	51.3			
1	2.5	0.00	0.00	0.88	2.44	0.98	0.92	62.31
2	3.0	0.00	0.00	0.48	2.10	0.95	0.50	56.03
3	3.5	0.00	0.27	0.53	2.33	0.92	0.55	60.66
4	4.0	0.00	0.21	0.42	2.17	0.91	0.44	57.92
5	4.5	0.14	0.24	0.62	2.53	0.93	0.46	64.07
6	5.0	0.15	0.25	0.79	2.74	0.95	0.52	67.61
7	5.5	0.13	0.21	0.66	2.55	0.94	0.43	64.26

W values in *Scabiosa* crops calculated on the basis of individual density and leaf number relatedness

Nr	d_{max}	W				r	C	V_{max}
		5.7	9.4	18.5	51.3			
1	2.5	0.00	0.00	0.10	0.29	0.90	0.11	12.15
2	3.0	0.00	0.00	0.06	0.26	0.83	0.06	11.95
3	3.5	0.00	0.03	0.06	0.27	0.81	0.06	12.06
4	4.0	0.00	0.03	0.05	0.26	0.79	0.05	11.98
5	4.5	0.02	0.03	0.07	0.28	0.81	0.05	12.13
6	5.0	0.02	0.03	0.08	0.29	0.84	0.06	12.22
7	5.5	0.01	0.02	0.07	0.28	0.82	0.05	12.14

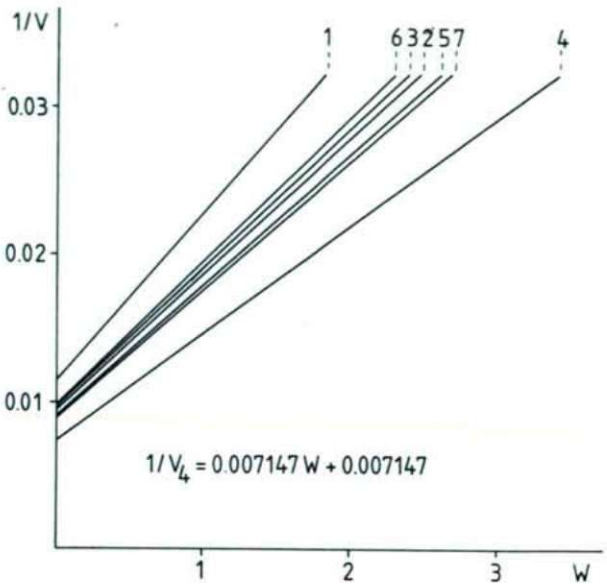

Fig. 1. Regression curves on the basis of the dry masses of *Plantago indica*.

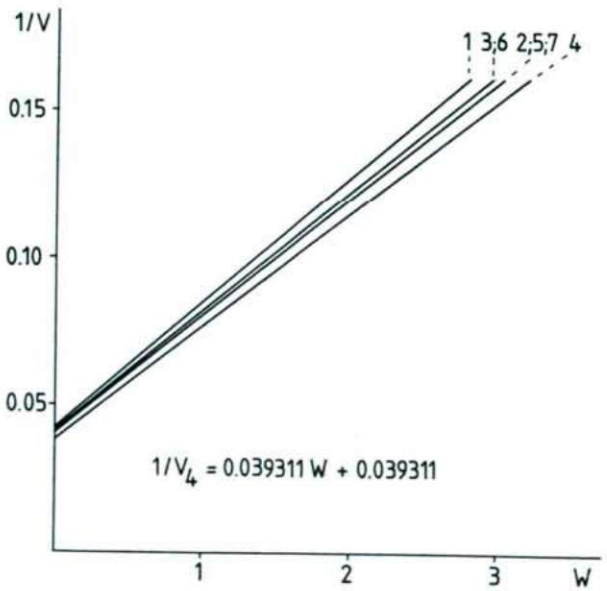

Fig. 2. Regression curves on the basis of the leaf numbers of *Plantago indica*.

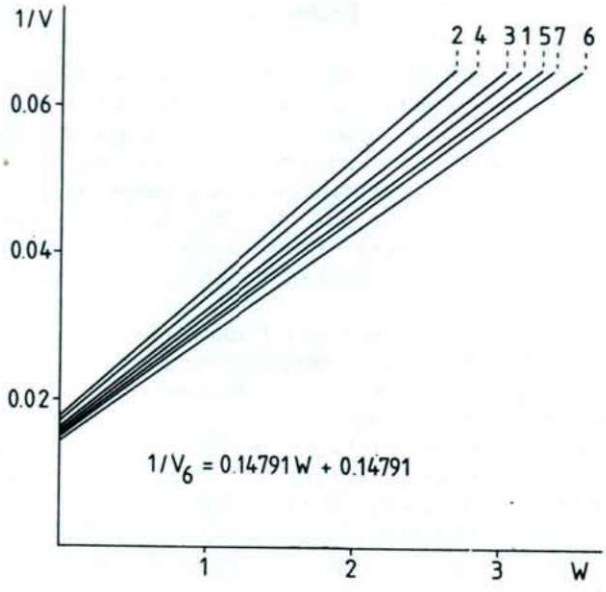

Fig. 3. Regression curves on the basis of the dry masses of *Scabiosa ochroleuca*

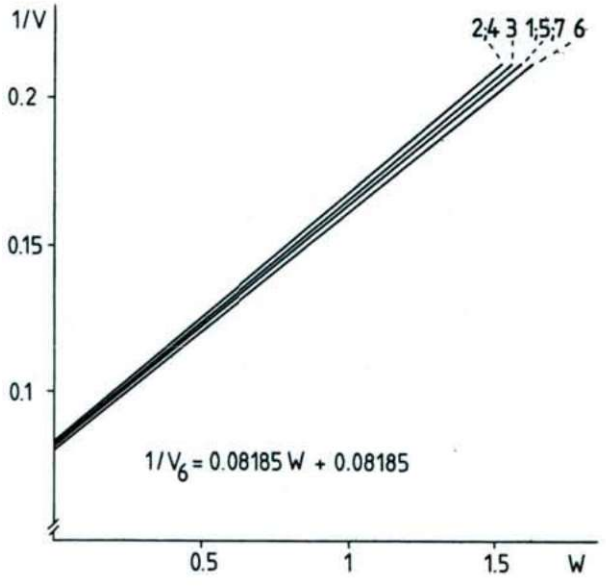

Fig. 4. Regression curves on the basis of the leaf numbers of *Scabiosa ochroleuca*.

Evaluation

The log/log transformation of the plant individuals' dry mass-plant density function is suitable for determining the maximal distance of the interaction of plant species. However, this estimation requiring two regression analyses demands several (8—10) crops of various density, furthermore, it is also necessary for the distance of the plant individuals to be greater than the distance of the interaction in the case of at least two most thinly sown crops. In case when these terms — mainly the latter one — are not fulfilled, the analysis cannot be accomplished since one of the two intersecting straight lines will be lost and thus the sought point of intersection will not be obtained.

The neighbourhood-model is suitable for approaching the maximal distance of competition from few samples. The reciprocal of the average individual weights was illustrated in the function of the W-values calculated on the basis of this model. According to the performed experiments, it can be determined that it was that d_{max} distance grade which approximated the competitive distance the best, in which the correlation of the regression curve was the best. However, the question can firstly be decided by where the V_{max} value is the highest.

In the case of *Scabiosa ochroleuca* the correlation coefficient was the greatest at $d_{max}=2.5$ cm, but not the V_{max}-value. The log/log transformation also supports the $d_{max}=5.0$ cm approach.

In the case of *Plantago indica* the maximum of both values coincided, and the approached distance was 4.5 cm.

The distance at which the individuals of a plant population of given age start to show interaction can also be approached from small number of samples. In such case that distance grade should be determined where the dry masss — or other densitydependent parameter — of the average plant individual assumes maximal value. In such manner the analysis can be performed in the case of populations of various distribution type, nevertheless the individuals of the population are required to be of the same age.

The behaviour of the two species having various phenological rhythm was rather similar in the first two phenophases. During the time of the experiment self-thinning was not experienced at either of the populations, the competitive interaction manifested in the volume of the average dry mass and the average leaf count of the individuals of crops of various density.

Their reproductive allocation would presumably also similarly reflect the density dependence of the interaction, using monoculture furtheron.

Nevertheless, under natural circumstances the members of the plant communities at the sandy grasslands regulate each others density by comprehensive interactions, the effect of which could be measured best in the ratio of the reproductive organs. Further studies are necessary, however, to be able to answer these questions.

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RELATIONSHIP OF THE MENARCHEAL AGE OF CITY-GIRLS WITH SOCIO-ECONOMIC FACTORS

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Abstract

Authors studied the menarche beginning and its relationship with socio-economic factors in the case of 10—18 years old Szeged (South Hungarian) girls, on the basis of data collected with status quo method. A total of 4963 city girls were questioned and the menarcheal age was analysed on the basis of 11 factors.

The median calculated with the probit analysis was found to be 12.68 years. The first menstruation showed monthly and seasonal fluctuation. There is relationship between the time of girls' first menstruation and the girls' order of birth, total number of sibs, number of living sisters, size of the place of birth regarding mothers and both parents, education and occupation of the mothers, resp.

The coincidence of the month of birth and month of menarche of the girls occured in 10.25%. The frequency of those whose menstruation was irregular even one year after puberty was 7%.

Key words: menarche, socio-economic factors, city girls.

Introduction

Data are at disposal for over 200 years regarding the physiological maturation of girls (HALLER, 1775). At the beginning, observations restricted only to the determination of the time of menarche, in the past decades, however, the phenomenon has been studied in connection with the most varied factors. In Hungary the first larger sample was published in 1963 (BOTTYÁN et al., 1963), comprising 7000 Hungarian girls. Today there are many observations and publications concerning the menarcheal age of the Hungarian girls. Nevertheless, neither in Hungarian, nor in foreign special literature, no examples are found in respect to the accomplishment of the collection of data besides six somatic characters expanded simultaneously to 24 socio-economic factors — firstly relating to family factors — in the case of a group of girls living in a well defined geographical region or within an administrative unit.

Therefore, we decided to perform detailed studies on the beginning of menarche and its connection with socio-economic factors, related to 10—18 year old girls living in the county of Csongrád.

Sample and methods

The reviewed results were achived within a larger research program, the detailed description of which has been reported earlier (FARKAS et al., 1983).

Here, we only wish to mention that the data of 29,879 girls aged from 10—18 were collected between February 23, 1981 and February 10, 1984. The majority (16,679) of the girls are from the county of Csongrád, 4,963 of them live in Szeged.

The data collected with status quo and anomymous questionnaire method were evaluated by R-40 type computer using the Osiris program package. The median was determined with probit analysis.

The changes in body measures are not discussed here since they have already been reviewed in an earlier paper (FARKAS, 1983).

Results

BEGINNING OF MENARCHE. — From 4,963 girls the menarche took place in the case of 3,088 during the period of the collection of data. It occurred earliest at the age of 8 years — in one single case — and after 16 years of age in 4 cases.

Taking for a base that the normal time interval of the menarche beginning is between the years 9—16 — at least in the case of the Hungarian girls — (SAS and KOVÁCS, 1984), it could be determined that too early menarche occurred only in two cases and that too late occurred in the case of four girls.

MENARCHE-MEDIAN. — 12.68 years was obtained as median, the 95% confidency interval of which was 12.18—13.18 years. Considering our earlier collection of data from Szeged as well (FARKAS, 1962, 1969), the following medians were determined:

Year of the study	Sample size	Median
1958/59	841	13.20
1961	1469	13.03
1966/67	774	12.73
1981/82	4963	12.68

A decrease is observable compared to the earlier data, although its rate has significantly slowed down in the past 15 years.

MONTHLY AND SEASONAL DISTRIBUTION OF MENARCHE. — On the basis of the admitted data the most frequent occurrence of menarche was in the months January (13.05%), August (13.01%), June (10.38%) and July (9.45%).

Likewise, the months January and August were also found to be the highest frequency in an earlier study (FARKAS, 1962).

According to the survey in 1981/82, the menarche beginning was 27.55% in the winter months, this being 39.35% earlier (between 1958—1961) (FARKAS, 1962).

As one of the causes of this change it could be mentioned that during the last 20 years many people moved to Szeged, the migration was great. In Western Hungary the relative frequency of the menarche beginning in the winter months is lower (EIBEN and BODZSÁR, 1970), nevertheless, seasonal fluctuation can be observed there as well. This phenomenon had been described 50 years ago (ENGLE and SHELESNYAK, 1934), thus it is characteristic not only for the Hungarian girls.

As another cause, an observation could be mentioned according to which winter accumulation is characteristic only for the city girls (KOWALSKA et al., 1963) and Szeged can also be ranked among this settlement category. In our case, however, the correctness of this assumption can only be decided after we have evaluated the data of girls living in smaller country settlement.

Out of 3,088 girls 2,966 remembered the month of menarche, 122 girls — 5.9% of those menstruating — were only able to tell the year of menarche one-two years after its beginning. Without a doubt it refers to the insufficient level of the sexual education.

In the followings a review is given of the development of the girls' menarche median according to a few socio-economic factors. The results in this regard are summarized in Table 1.

BIRTH ORDER OF GIRLS. — In our sample the difference between the median of first and third born girls was 0.37 year, i.e. the third born girls start to menstruate about 1/4 year later than the first born girls (Table 1, I. row).

This does not seem to be a great difference. BODZSÁR (1975) obtained similar result in the case of girls from Székesfehérvár (town in Central Hungary), and EIBEN (1972) received dissimilar result for Western-Hungarian girls.

Mainly Hungarian data are at disposal concerning the correlation between birth order and menarche (BODZSÁR, 1975, 1977; EIBEN, 1972; FARKAS, 1980, 1982), nevertheless, connection between the two phenomena was also observed for German girls (RICHTER, 1980).

TOTAL NUMBER OF SIBS. — Here are observations for a long time in respect to the relatedness of the number of sibs and the time of puberty of girls (BOLK, 1923, 1926). Most of the authors take the position that number of sibs and the time of puberty of the girls are in close connection with each other, furthermore, that high correlation could be determined between them (ROBERT, 1977).

The median also increased in the case of girls from Szeged on the basis of the number of sibs (Table 1, 2. row). Between the median of those without any sibs and those having three ones the difference was 0.47 year.

NUMBER OF LIVING BROTHERS. — When taking only to brothers into consideration from the sibs, such a slight difference was obtained between the medians that no correlation could be presumed between the two factors on its base (Table 1, 3. row).

NUMBER OF LIVING SISTERS. — The difference was higher when considering only the number of sisters. The difference was 0.23 year between the median of those without any sisters and those having two, with the observation of a steady increase (Table 1, 4. row).

SIZE OF THE PLACE OF BIRTH OF MOTHERS. — There are no comparative data at disposal from other sources regarding the connection between the size of the place of birth of parents and the date of birth of their daughters

In case of girls from Szeged the median did not show a steady change in conformity with the number of inhabitants of the birth-place of the mothers. The difference between the median of the daughters of mothers born in the largest and smallest populated settlements was found only to be 0.10 year. At the same time, however, the lowest (12.27 years) median was found for daughters of mothers born in settlements with 50—100 thousand inhabitants and the highest (12.87 years) was found in the case of the 5—10 thousand populated settlements. Accordingly, the difference was 0.60 year corresponding to more than half a calendar year (Table 1, 5. row).

Table 1. Change of menarche-median in the case of various socio-economic factors

Studied factors		Total cases	Median	95 p.c. conf. interval.
1. Order of birth	First born	2860	12.67	12.59—12.74
	Second born	1550	12.65	11.92—13.38
	Third born	300	13.04	11.90—14.19
2. Number of sibs	No sibs	985	12.61	12.39—12.82
	One sib	2807	12.65	12.45—12.86
	Two sibs	743	12.74	12.28—13.19
	Three sibs	214	13.08	12.22—13.93
3. Number of living brothers	No brothers	2536	12.67	12.15—13.19
	One brother	1980	12.69	12.53—12.85
	Two brothers	307	12.66	12.07—13.26
4. Number of living sisters	No sisters	2666	12.63	12.55—12.71
	One sister	1809	12.70	11.57—13.82
	Two sisters	335	12.86	12.46—13.26
5. Size of mother's birth-place	100 000—200 000	2085	12.60	11.39—13.81
	50 000—100 000	222	12.27	11.86—12.68
	10 000— 50 000	635	12.69	12.42—12.97
	5 000— 10 000	564	12.87	12.09—13.65
	below 5000	1012	12.70	12.51—12.90
6. Size of father's birth-place	100 000—200 000	2137	12.68	10.25—15.07
	50 000—100 000	202	12.69	11.48—13.91
	10 000— 50 000	582	12.66	12.27—13.05
	5 000— 10 000	534	12.72	12.52—12.92
	below 5000	944	12.73	12.26—13.19
7. Size of both parents' birth-place	100 000—200 000	1176	12.59	9.75—15.34
	10 000— 50 000	138	12.79	12.01—13.57
	5 000— 10 000	147	12.62	11.98—13.26
	below 5000	350	12.93	12.71—13.15
8. Education of mother	Primary school studies unfinished	242	12.88	12.57—13.19
	Primary school	1773	12.73	12.64—12.82
	Trained for skilled work	465	12.61	12.43—12.79
	Secondar school	1788	12.65	12.52—12.79
	College or University	612	12.59	11.29—13.89
9. Education of father	Primary school studies unfinished	220	12.76	12.29—13.23
	Primary school	1512	12.74	12.55—12.93
	Trained for skilled work	708	12.52	11.88—13.17
	Secondary school	1408	12.70	12.00—13.39
	College or University	945	12.65	12.30—13.00

Table 1. cont.

10. Occupation of mother	Industrial manual worker	667	12.82	12.35—13.28
	Other manual worker	1467	12.68	12.38—12.97
	Intellectuel with secondary school education	1814	12.65	12.56—12.73
	Intellectuel with higher education	547	12.58	11.27—13.90
	Housewife	190	12.67	12.03—13.32
	Retired	139	12.71	12.23—13.18
11. Occupation of father	Industrial manual worker	1482	12.70	12.05—13.36
	Agricultural manual worker	99	12.53	12.08—12.18
	Other manual worker	1038	12.65	12.42—12.89
	Intellectuel with secondary school education	958	12.64	12.51—12.76
	Intellectuel with higher education	916	12.66	12.43—12.88
	Retired	183	12.72	11.09—14.35
	Dead	138	12.45	11.28—13.64

SIZE OF THE PLACE OF BIRTH OF FATHERS. — On the basis of the size of the birtplace of fathers such a slight difference was obtained between the menarche-median of their daughters that according to this it is presumed that in our sample the size of the birth-place of fathers does not play role as an influencing factor in the beginning of menarche of their daughters (Table 1, 6. row).

SIZE OF THE PLACE OF BIRTH OF BOTH PARENTS. — It was also studied how the menarche-median of girls developed if both parents originated from settlements of the same size. In this regard those girls reached maturity later (their median being 12.93 years) those parents originated from settlements having a population lower than 5 thousand. However, those girls reached puberty earliest (with a median of 12.59 years) whose parents were born in settlements having 100—200 thousand inhabitants (Table 1, 7. row).

The difference of 0.34 year does not seem to be great, nevertheless it is noteworthy.

The tendency of the increase of the median was observable towards the low populated settlements. This may also be due to the varying number of girls who could be classed among the different settlement categories.

Similar results were gained on the basis of the earlier Hungarian data (FARKAS, 1979).

EDUCATION LEVEL OF MOTHERS. — Relatively few authors have studied whether there is any relationship between the education of parents and the time of puberty of their daughters (BIELICKI, 1982; DEMERDŽIEV—LAZAROV, 1978; RICHTER, 1973). The conclusions are not synonymous.

In the case of the girls from Szeged the education of parents was grouped into five categories (FARKAS et al., 1983). According to this the menarche-median of those girls was higher (12.88 years) whose mothers did not finish their primary school studies. Those girls reached maturity earliest (12.59 years) whose mothers have higher grades of education. The difference between the lowest and highest education

categories was found to be 0.29 year (Table 1, 8. row). Since the median showed steady change, disregarding one single smaller difference the education of mothers should be treated as an influencing factor.

EDUCATION LEVEL OF FATHERS. — Grouping the girls according to the level of education of their fathers, the difference between the median of the daughters of fathers having the highest and lowest education was only 0.11 year. However, the difference between the highest and lowest median was 0.24 year. The medians decreased with the level of education.

Similarly to the case of mothers, the daughters of fathers who received training for skilled work were only exceptions (Table 1, 9. row).

OCCUPATION OF MOTHERS. — Very few authors state that there is no connection between the occupation of mothers and the time of puberty of their daughters (BERBROCINER, 1964; ROBERTS—DANN, 1967; ROBERTS et al., 1971). Others think it to be the strongest influencing factor (MILICER, 1968). The experience could be regarded as general that the daughters of intellectual parents reach puberty earlier than the children of manual workers. This is also supported by data from Hungary (BODZSÁR, 1975; EIBEN, 1972; FARKAS, 1980).

Our results in respect to the girls of Szeged also refer to the fact (Table 1, 10. row) that the girls whose mothers are mental-workers reach maturity the earliest (median: 12.58 years) and those of industrial manual worker mothers mature the latest (median: 12.82 years). The median of the girls whose housewieves or retired cannot be adapted to this series. It is obvious that a great variety of original occupations could be ranked among the two categories and the development of the medians may be in connection with this.

OCCUPATION OF FATHERS. — The lowest median (12.45 years) was found for the daughters of fathers who have died, in this case the occupation is also not known exactly. The highest median (12.72 years) was obtained for the daughters of retired fathers. The difference between the two end values was 0.27 year (Table 1, 11. row). In respect to correlation, it would be difficult to take a position in any regard by analysing the medians obtained on the basis of the differing elemental number of the various occupational groups.

CONNECTION BETWEEN THE MENARCHEAL MONTH OF MOTHERS AND DAUGHTERS. — Authors have referred to this connection for a long time (BOLK, 1923, 1926; BOAS, 1932). TANNER (1962) defined its degree with a correlation coefficient of 0.40. However, we have no date from other sources on any observations regarding the coincidence with monthly punctuality of the menarche of mothers and daughters.

Studying the two events, we received the data that the menarcheal month of mother and daughter coincided in 203 cases out of 2831 girls (7.05%). The result of the chi-square test on 99.9% probability level allows the assumption that the coincidence of the two phenomena is not entirely accidental. Nevertheless, at the same time it should also be mentioned that the incidence of 7.05% is below the expected value in case of even distribution.

COINCIDENCE OF MENARCHEAL MONTH AND BIRTH MONTH. — Many references are found in special literature to the coincidence of the girls' menarcheal and birth month. It is a fact that presuming even distribution the coincidence of the two phenomena is

found in an incidence higher than 8.33% expectable in theory to fall to the same month. Despite this, certain authors do not presume any correlation between the two phenomena (BOILÉN—BENTZON, 1971), while others hold the coincidence verifiable by statistical test, too (BARIŠIĆ—GAVRILOVIČ, 1974). In the case of Hungarian girls the frequency of the coincidence varies from 8.15 to 14.86% (FARKAS, 1971). On the other hand, foreign authors report on values between 11.53 and 15.88%.

In our sample, coincidence was demonstrable in 304 out of 2966 cases, corresponding to a relative frequency of 10.25%. This could be taken as verifiable on 99.9% probability level with the chi-square test.

REGULARITY OF MENSTRUATION. — During the course of the collections of data the girls already menstruating were also questioned in regard to the regularity of their menstruation. In 271 out of 2852 evaluable data (9.5%) the girls questioned remarked their menstruation as not being regular. Out of them 70 girls were 14 years old, or younger. In their cases the irregular menstruation cannot be regarded as pathologic, considering the median of 12.68 years. The remaining 7.05% also indicates a rather great frequency, the importance of which can only be understood actually if taking into consideration that only few of these girls know they should turn to a medical specialist in such case. This again refers to the inadequacies of the sexual informative campaign.

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PALEOPATHOLOGY OF THE AVER-AGE BETWEEN THE DANUBE AND TISZA RIVERS

(Thesis of Dissertation for Candidate Degree)

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I. THE PROBLEMS OF PALEOPATHOLOGY, THE OBECT OF THE DISSERATION

Paleopathology — similarly to the other sections of paleoanthropology — is one of the chains in the path leading to biological reconstruction, which — together with the results of other sciences (archeology, historical science, written sources, etc.) — leads to the complex characterization of the community. Setting out from our knowledge on medical history and the medical sciences of today, we can even set up general principles and may have ideas about the development of a certain phenomenon or disease, but we actually know only very little about what happened in reality. The explanation to this is that the pathological studies on the skeletal findings of populations originating from various archeological periods are rather limited and are full of certain difficulties owing to the nature of the studied material:

- — the traces of only relatively low amount of specific diseases can be identified on the bones, accordingly the majority of the pathological observations are related to non-specific diseases;
- — the duration of the disease and the anamnesis are not known;
- — at times the various diseases may produce the same morphological changes in the bone, and conversely the same kind of disease may produce various deformations in other cases;
- — it is difficult to decide which pathological process should be regarded to be the basic disease and which occurred as complication;
- — fossilization and the late postmortal phenomena (effect of soil, animals, plants) conceal or even imitate the actual prognostic symptoms.

Considering the difficulties and problems of paleopathology the object of the dissertation was drafted in the followings, without the aim of completeness:

1. description of certain pathological character-complexes of a larger number of skeletal findings from a given geographical area from the same centuries, and as far as possible, the description of their specific and non-specific disease units; furthermore the outlining of their pathomechanism, etiology and differential diagnosis on paleonosological basis;

2. specification of bone deformations or characteristics which are less known or seem to be important in the medical sciences of today;

3. defining the question whether the same manner of living could be concluded from the similarities and cumulative occurrence of the pathological deformations.

II. Materials and Methods

The skeletal findings analysed in the dissertation originate from the Avar series between the Danube and Tisza rivers. One part of these finds have already been processed apart from the detailed paleopathological analysis by classic anthropological methods and according to other viewpoints.

From the total 1960 skeletal findings (42 sites) studied 721 were males, 786 were females, 423 were children and juveniles, the number of adults of undefined sex was 30. When studying every finding at disposal the candidate set out from the deviations from the total anatomical characteristics of the "homo universalis" regarded as normal.

First of all the question had to be decided whether the deformation was of postmortal origin or not. After excluding this, attempt was made to clarify the nature of the morphological change, the anatomical variation, the minor developmental abnormality, the actual disturbance of growth or pathological alteration in question. This was followed by the detailed description of the phenomenon. The morphological diagnosis was set up on the basis of the observed morphological picture and the adequate studies of special literature.

X-ray pictures were prepared for more precise diagnosis.

Histological analysis (preparation of polished specimen or section or scanning electron microscopic study) was performed examining the more precise morhological characteristics of a phenomenon.

The changes determined on the basis of morphology, X-ray and in certain cases histological as well as scanning electron microscopic studies, were grouped according to diseases. The anatomical variations and the minor developmental abnormalities were not dealt with since the majority of them do not belong to the concept of paleopathology. In some part of them however, it cannot be devided or at least excluded whether their presence displayed harmful effect on the organism of the person or whether they formed a transition towards the more severe disturbances of growth, therefore in this sense they can be ranked amongst the wider field of paleopathology. Among them the occurrence of only two types of characteristics — irregular enamel formations and the Stafne defect on mandible was studied.

Deformations other than anatomical variations and minor developmental abnormalities were ranked among the more restricted field of paleopathology, and the book of Steinbock was the base for setting up their nosology, although some modification was made due to the characteristics of the studied material.

Accordingly the material of the dissertation is discussed in the following arrangement:

Pathological deformations of wider sense
- — irregular enamel formations
- — Stafne *defect* on mandible

Pathological defects of narrow sense
- — developmental anomalies
- — traumatic lesion
- — non-specific inflammation

— tuberculosis
— haematologic disorders
— joint disease
— other diseases

Due to the special problem of paleopathology (e.g. the whole skeleton is not at disposal, etc.) statistical method could not be applied in every case for evaluating the causal connections between the various phenomena and diseases as well as for the exact determination of their incidence (except when they were found localized on a determined place of the bone or teeth). This should be complemented with the fact that there are also such diseases, the occurrence of which is extremely rare or even unique.

III. Summary of results

1. The two main forms of enamel formations appearing on the cervical and root-surface of teeth were the enamel tongue and the enamel pearl. 2905 molars were studied. The enamel tongue was the most frequent on the lower M_2 (33.8%), and the enamel pearl on the upper M_2 (45.5%). The incidence of the former was lower while that of the latter was identical compared to the clinical data. There were no differences between sexes in respect to the enamel formations of irregular location according to a statistical evaluation. The enamel tongue is the anatomical variant of the enamel edge; the enamel pearls — particularly those of dentin or dentin-pulp components — can be regarded as the microforms of geminate-teeth, thus they are developmental anomalies.

2. The Stafne *defect* on mandible is an indenture on the lingual surface of the corpus mandibulae between the last molar and the angulus mandibulae. The frequency of the defect was 1.2% regarding 1495 mandible, being somewhat higher than the clinical data. The defect only showed higher incidence in the case of adults and males. The Stafne defect can be regarded as a developmental anomaly which is in relationship with the localized deficiency of the growth of mandible. It is the consequence of undefined environmental or genetic factors manifested in the adult age, and this is made even more severe by the hypertrophy of an ectopic gland or other tissue type.

3. The developmental anomalies were grouped according to their anatomic region. From these *sphenocephalia, palatoschisis* and *luxation (dysplasia) coxae congenitae* are significant as they are rare diseases. From the viewpoint of incidence the anomalies of vertebrae, *sacralisation* and *spondylolysis* are important. The evaluation of the developmental anomaly as well as the drawing conclusions regarding relationships can only be made possible in the case of well excavated cemeteries and well preserved, entire bone finds.

4. The traumatic lesions were divided into three groups (*fractures, dislocations* and bone injuries caused by sharp instruments). Among them the significance and frequency of fractures is the greatest, which were further grouped according to their various forms. Within the changes caused by sharp instruments *trepenation* had the greatest significance.

5. *Osteomyelitis* and *periostitis* belong to the nonspecific cases of inflammation. In our findings *osteomyelitis* was few while relatively more cases of *periostitis* occurred. According to the possible etiology *osteomyelitis* was divided into three

smaller groups. Numerous factors may play role in the etiology of *periostitis* appearing in independent form.

6. Among the various forms of *osteotuberculosis spondylitis* and *coxitis tuberculosa* were significant in the studied material, these diseases were found to occur in the findings of the series from the Southern areas.

7. From the haematologic disorders the bone symptoms of *anemia* should be emphasized appearing in the form of *porotic hyperostosis* on the skull. The three types of this deformation can be distinguished well morphologically and histologically. Taking into consideration the wide variety of environmental factors, *porotic hyperostosis* should be interpreted as the osteological symptoms of anemia originating from the lack of ferruginous diet. The incidence of this phenomenon was high in the studied finds (22.6%).

8. Evaluating the joint diseases the main viewpoint was that the inflammatory and regressive pathological processes produce symptoms similar or identical to each other. The deformations were ranked into two large groups. *Osteoarthritis* was of relatively lower, and vertebral *osteophytosis* was of higher frequency. Apart from these we can also speak of secondarily developed *arthritic deformations* developed on the effect of *trauma* and *infection*. In the case of joint diseases, therefore, we can only account on four types of deformations in our material: — based on the 7 divisions of MORSE — the *vertebral osteophytosis* was divided into three further groups according to the seriousness of appearance. The incidence of the deformation was somewhat higher in males, but in both sexes it was significant on the thoracal section, in the Maturus death age group.

9. The *tumors* and *osteologic symptoms* of the metabolic diseases *(osteoporosis)* were classed among the other diseases. *Osteoporosis* was determined morphologically and with the help of X-ray pictures. The *metastatic tumor* regarded as a rare clinical appearance was rather significant within the *tumors*. The etiology of *osteoporosis* is extremely multiple, definite stand is negligible.

10. On the basis of relationships between the diseases and phenomena the following rare and unique clinical pictures could be emphasized: *sphenocephalia, palatoschisis,* manifestation *vertebrae occipitalis, synostosis costarum* et *bifurcatio costae, hemivertebra thoracalis, osteomyelitis* following compound *fracture, trepanation, myositis ossificans traumatica, metastatic tumor;* the following deformations were less frequent: enamel formations of irregular location, STAFNE *defect* on mandible, *fissura* on the *sternum, luxation (dysplasia) coxae congenita, osteomyelitis, tuberculosis,* metabolic diseases; and the following were of higher incidence: *spina bifida occulta, synostosis thoracalis, sacralisatio et lumbalisatio vertebrae, spondylolysis verebrae lumbalis, fracture* marks, *periostitis, porotic hyperostosis, osteoarthritis, vertabral osteophytosis.*

11. With the exception of the STAFNE *defect,* the *vertebral osteophytosis* and the *haematological abnormalities* the differences between sexes were not significant. The former two deformations were more frequent in males, the latter one in females, although it is significant in the case of children and juveniles as well.

12. In respect to the cumulative occurrence of the deformations the habitude of the existing population could only be concluded from certain diseases (marks of *traumatic* lesions, interpretation of *porotic hyperostosis*).

IV. Practical utility of the results of the dissertation

1. The *fractures* of the studied findings are significant from the viewpoint of medical history. In the majority of the finds healed fractures were found which recovered without *axel-aberration* and functioning lesion, thus these peoples obtained great skill and experience in the curing *bone fractures.*

From the studies on the haematologic disorders the consequence could be drawn that *β-thalassaemia* could not originate from China and was not brought to Europe by the Mongolian invasion, since *porotic hyperostosis* was of high incidence in the examined Avar material and *anemia* due to deficient diet is made responsible as its etiology.

Concerning the evaluation of *osteomyelitis* it may be presumed that the spreading, virulence of pyogenic microorganisms or the resistance of the individuals probably differed at that time.

2. The pathological examination of the findings enlighten us on the animistic or disease-curing habits *(trepanation),* way of life (studies on *porotic hyperostosis*) and ethical attitude (patients with serious illnesses reached the higher age) of the population living in the Avar period, in archeological regard.

3. The pathological deformations may also be of significance to the medical sciences of our time: by the joint interpretation of their morphological appearance and X-ray picture; by the more detailed survey and analysis of certain phenomena: the presence of enamel pearl particularly when containing dentin or *dentin-pulp component,* too — may cause difficulties in dental treatment; the Stafne mandible cavity bears risk of pathological *fracture* (these latter two deformations have not been described in the earlier Hungarian paleoanthropological literature); furthermore, studies on *porotic hyperostosis* also call attention to the early stage of the disease, in which case the bone changes are not visible on X-ray picture, nevertheless, the histological and scanning electron microscopic studies proved that the process in question is the same.

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ACCELERATION — SEXUALITY CERTAIN CHARACTERISTICS OF THE SEXUAL LIFE AND PHYSICAL MATURITY OF 14—18 YEARS OLD SECONDARY SCHOOL CHILDREN

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Abstract

The accelerated social development of the 20th century brings the time of the sexual maturation earlier and sexual reaction-readiness of the young as well. Although acceleration has strongly slowed down nowadays, the sexual activity of the young is beginning much earlier and is also more intensive. (They begin their sexual life at the age of 15—16 on an average). The former facts are supported by a sexological survey and growth study carried out among school children from the county Csongrád (Southern Hungary).

At the end of the paper a summary is given of the facts thought by the author to result (with the exception of acceleration) in the earlier and more intensive sexual life of the young, compared to the previous generation.

Key words: acceleration, petting, sexual intercourse, orgasm.

Introduction

Ontogenesis is no other than the enactment in determined succession of the developmental information, its manifestation on the basis of the genetic program of the impregnated ovule. The genotype in interrelation with the environment jointly determine the prevailing reality from the prospective potential. The investigational results prove that both in human and domestic animal relations the embryonal and postembryonal effects are important in the enactment of the genetic information. Since this recognition made at the end of the last century, the effect of environment on development is also considerably tried to be ensured consciously. (For example deliberate family planning, pregnant care, medical care and improvement of social conditions, formation of correct dietary habits, etc). All these have jointly resulted in the accelerated physical development of the 20th century, being mentioned as secular acceleration. This means that "today more abilities might prevail and earlier, than at any time so far" (NAGY, 1969).

The young are higher, have greater weight and become mature sexually earlier than their ancestors of the 19th century. BRYAN and GREENBERG (1952) have proved that children reaching maturity earlier are higher and stronger than their mates.

The scientists studying the facts calling forth acceleration are mainly on the same opinion in respect to the multifactoral character as well as the causes revealed so far. The accelerative hypotheses considered by WALTER (1978) are as follows:

1. Heliogenic-effect hypothesis of KOCH (1935)
2. Urbanization effect (DE RUDDER, 1943, 1960)

3. Selection hypothesis (BENNHOLDT—THOMSEN, 1942),
according to which the vegetative more unstable rural people are stimulatingly affected by the urban stimulatory reactions.

4. Disintegration of genetic isolates (SCHAEUBLE, 1954; NOLD, 1963)

5. Change in dietary habits (LENZ, 1944) both from quantitative and qualitative viewpoints (protein, vitamin, mineral salts).

From his studies carried out on couples of various degrees of relationship, THOMA (1960) came to the conclusion that the determinative role of the genetic effect in sexual maturity falls between 72.2 and 88.2%.

In his comprehensive essay, GRIMM (1966) gives an analysis of the accelerative factors determined by SCHLÜSSEL (1965). In comparison to the classification of WALTER, they mention two new factors; "Decrease in illness in early childhood" and — although not emphatically — "The influencing role of sexual sphere", referring to several authors and their own studies.

The acceleration of somatic development ensures favourable conditions for the acceleration of psychical puberty, too, which to a certain extent also has stimulating reaction on the somatic acceleration. All this can be stated despite the fact that in human relations there is uneven development, i.e. negative allometry between the nervous system and the rest of the body (NAGY, 1969), this making the growth acceleration of the young a social problem at the same time. It is evident that those young people who menstruate and experience pollution earlier, start to think of sexual life and are even familiar with these questions earlier (RÖSLER, 1963), and thus also show interest sooner in the practical realization of sexual intercourse.

Materials and methods

Since the rate of acceleration is presumably also influenced by the climatic factors besides the social and biological effects, only the data of surveys carried out at identical areas have been used. Due to the fact that there are no data at disposal regarding the sexual maturity of boys from the environs of our habitation (such data are few even in international literature because of the difficulties of the objective measurements), the process in only demonstrated in the case of girls.

During the course of the last two decades FARKAS et al. performed two large-scale growth studies in Szeged and the county of Csongrád. They studied 1,136 girls from Szeged in the 1966—67 school-year (FARKAS, 1969) and 4,963 in the 1981—82 school-year (FARKAS et al., 1985), using the same methods. From the study results we put forth only those data which are the most important in respect to sexual maturity, thus the menarche medians, as well as the age values of the 50% developmental stage of the breast (mamma) and pubic hair (pubes).

The sexological survey carried out by the author in 1982 in the county of Csongrád among secondary school students (aged 14—18) serves as the demonstration of the sexual activity of the young people. During the course of this survey information was obtained from 7,409 students by anonymous questionnaire method, from which the data of 7116 students could be evaluated. (The rest of the forms were not filled out (71) or were of no use due to misleading data (222)). The coding of the questionnaires was carried out by two persons all through, and besides this the majority of unreliable data could be screened with the help of so-called control questions. The data were adapted to R-40 type computer and processed with the OSIRIS program-package (RATTENBURY and VAN ECK, 1973).

A few characteristics of the sample — comprising 42.63% of the county's students — are the followings:

distribution of students according to sex — boys 48.6%, girls 51.4%;
distribution according to school types — secondary school students 59.4% students of vocational training 40.6%;
students living in whole families — 79.2%;
distribution of parents' occupation: 65.7% of fathers were manual workers;

40.1% of mothers were manual workers;
17.5% of fathers had secondary school education;
this being 22.2% in the case of mothers;
8.5% of fathers, and 5.1% of mothers had higher education.

Most of the social data suitable for comparison correspond to the county and even the national data with deviation of only few per cent. Therefore, our sampling could be regarded as proportional, despite the fact that participation in the survey was voluntary.

Results and discussion

The first menstruation (menarche) is the most exact sign of sexual maturity, puberty in the case of girls. While in Hungary it occurred between 15—19 years of age during the 19th century, on the basis of the data by FARKAS (1969) the menarche median value came to 12.73 years in 1966—1967 in Southern Hungary. At the same time the 50% level of adulthood maturity was 12.4 years regarding breast development (mamma) and 13.85 years in respect to pubic hair (pubes).

Former author received the following results from the same area in 1981—1982: menarche 12.68 years (FARKAS et al., 1985), mamma 12.95 years; pubes 12.6 years (FARKAS, data not published yet).

The data (with the exception of breast development) prove that although in slower rate, the start of sexual maturity has shifted to an earlier period even in the past one and a half decades. The slackening (moreover, regarding certain marks the stagnation) of acceleration could be explained by the fact that the maximal realization of the developmental program stabilized in the genes is hindered by less and less factors.

The experiences of every-day life and the results of our survey also demonstrate that not only the starting of sexual maturity, but even the beginning of sexual activity shift to earlier and earlier period, and at the same time the intensity increased as well. The enhancing eroticism experienced in the spheres of mass (public) communication, the more and more optimal joint presence of the somatic and psychical conditions bring the development of sexual reaction ability and fitness for accepting sexual experience to an earlier period (NÉMETH and GALAMBOS, 1984b). This is the worldwide phenomenon of the 20th century.

On the basis of the data by TERMAN (1938) in the USA 90% of the women and cc. half of the men got married without previous heterosexual relations at the beginning of the century. This proportion decreased to 40% for women and to 20% for men by the middle of the thirties. Similar observations were made in Europe. For example, according to the survey of SCHMIDT and SIGUSCH (1970) carried out in 1969 in the German Federal Republic, the ratio of university students having sexual relations averagely increased by 18—23% regarding males (18—20 years of age) and by 3—5% regarding females — compared to the only three years earlier (1966) data of GIESE and SCHMIDT. This latter fact also proves that the earlier starting of sexual life in the case of biologically developed the young people can be attributed to social effects. The same could be said for the young of puberty-age, since earlier sexual maturity only gives objective possibility for starting sexual life, however, the prevailing reality is determined by environmental (social) effects.

Sexual experiences of the young people

In the followings, a few data demonstrate the level of sexual experience of secondary school students from the county of Csongrád, at the beginning of the 80ies. The data could not be compared with previous ones since there are no survey data on this age group at disposal. Nevertheless, on the basis of estimations and personal experiences from schools, it could be stated that both the starting and activity of their sexual life surpass by far that of their mates of the previous generation.

On the basis of the study carried out by Németh and Galambos (1984a, 1984b) in 1982, the ratio of the young having intim heterosexual relations (easy-petting, heavy-petting, sexual intercourse) at the time of their 14th year was 57.1% for boys, and 62.8% for girls; being 87.9% and 94.0% in the case of the 18-year-old youths.

One third (35.5%) of the students already had heavy-petting (genital manipulation) experiences, within this group this meant substitute activity for sexual intercourse in 32.3% of the boys and 58.2% of the girls.

25% of the students had experiences of sexual intercourse (24.0% for boys, 25.8% for girls). As for function of age, the results obtained for the two sexes are as follows: in the case of boys the ratio of students already having sexual intercourse increased from 5.8% at the 14th year to 36.5% at the 18th year; in the case of girls this increase was from 4.8% to 51.0%. The median value of the time-point of the first sexual intercourse is 15.39 years for boys and 15.9 years for girls (Fig. 1.). It could be determined that the girls start their sexual life about half a year later, but then considerably leave their boy age-class behind.

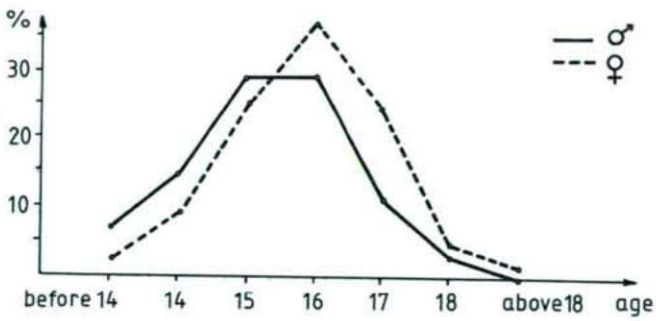

Fig. 1. Median of first sexual intercourse

Motive pattern and success of first sexual intercourse

Studying the motives of the students' first sexual intercourse it should be determined that factors of society motivated the majority of the boys, while emotional reasons prevailed in the case of the girls (Table 1.). This, too, verifies the statement of Kon (1979) that boys are firstly motivated to start sexual life by curiosity, sexual necessity and self-justification, while girls set a higher value on emotional intimacy and regard sexual relations as the strengthening of the psychical connection with boys rather than as purpose in itself. It should be mentioned, however, that nowadays this tendency is decreasing more and more and greater majority of the girls — especially under adequate circumstances — are even capable of establishing sexual relations with boys merely through sympathy.

Table 1. Motives of first sexual intercourse

Motives	boys		girls		total	
	n	%	n	%	n	%
curiosity	190	22.8	85	9.5	275	15.5
society atmosphere	113	13.6	31	3.3	144	8.1
mildy drunken state	111	13.3	43	4.5	154	8.7
"I wanted to seem modern"	8	1,0	3	0.3	11	0.6
keeping of partner	19	2.2	48	5.1	67	3.8
true love	322	38.7	669	70.9	991	55.8
interests	16	2.0	3	0.3	19	1.1
compulsion	4	0.5	48	5.1	52	2.9
question not answered	49	5.9	14	1.5	63	3.5
total	832	100.0	944	100.0	1776	100.0

In both sexes the circumstances of the supervention of the first sexual intercourse are characteristic of being incidental (55.9% for boys and 54.8% for girls). Only 43.4% of the girls who already had sexual intercourse made plans (prepared) consciously for the first occasion in advance.

22.3% of the students were disappointed in the first sexual intercourse (13.8% of boys and 28.3% of girls). Studying the motives of the disappointed students it was determined that firstly the fulfilment (giving of pleasure) falling short of previous expectations played role as cause of disappointment on behalf of the partners (NÉMETH and GALAMBOS, 1984b).

It is characteristic of the quality of the first sexual intercourse that 66.6% of boys and 24.1% of girls declared to have had the feeling of orgasm. Despite the well-known orgasm difficulties of women at the first sexual intercourse it is an important task of the adult society (parent, teacher, physician) to prepare the young people for pleasant as possible first sexual act, since as BUDA (1980) wrote: "the mode and nature of the first sexual attempts may be so strongly determinative that later the personality will get excited the most easily and most passionately by such or similar excitations, or seeks this very form of excitation as sexual object". Therefore, the first experiences exert strong effect on the further development of the personality, both in positive and negative directions. According to our opinion, too, these may open way for both the reception and improvement of more and more joyful sexual experiences but at the same time, might also orientate towards surfeit, frigidity, and indirectly even homosexuality.

Table 2. Frequency of matings of students ($n=1755$)+ having sexual intercourses previously

a) *boys*

frequency \ age	14		15		16		17		18		total	
	n	%	n	%	n	%	n	%	n	%	n	%
once	8	29.6	55	32.7	63	22.8	31	12.2	9	10.0	166	20.3
on few occasions	13	48.2	51	30.4	94	33.9	85	33.3	22	24.4	265	32.4
occasionally	3	11.1	43	25.6	72	26.0	76	29.8	28	31.1	222	27.2
relatively regularly**	2	7.4	6	3.6	33	11.9	48	18.8	26	28.9	115	14.1
question not answered	1	3.7	13	7.7	15	5.4	15	5.9	5	5.6	49	6.0
total	27	100.0	168	100.0	277	100.0	255	100.0	90	100.0	817	100.0
b) girls												
once	12	42.9	38	24.4	49	16.1	40	12.5	12	9.4	151	16.1
on few occasion	14	50.0	78	50.0	139	45.5	132	41.5	49	38.2	412	43.9
occasionally	—	0.0	13	8.3	11	3.6	19	5.9	8	6.3	51	5.4
relatively regularly**	2	7.1	23	14.7	96	31.5	127	39.6	58	45.3	306	32.6
question not answered	—	0.0	4	2.6	10	3.3	3	0.9	1	.08	18	2.0
total	28	100.0	156	100.0	305	100.0	321	100.0	128	100.0	938	100.0
both sexes together	55		324		582		576		218		1755	

* In the group broken down according to jears of age the elemental number of the active sample is less because a few students did not provide their birth date.

** E. g.: weekly, bi-weekly

FREQUENCY OF SEXUAL INTERCOURSE OF STUDENTS

Within the active sample ($n=1776$) it was also examined how frequently the students have sexual intercourse and how many partners they had so far. It can also be seen from Table 2 that — although the girls start their sexual life later — a rather high proportion (17—18th year) mate regularly.

Taking into consideration the frequency of the number of partners regarding those who had several sexual intercourses (Fig. 2), it could be determined that the sexual life of girls is rather characterized by regularity and small number of partners, that is, by emotionally more complete more balanced sexual behaviour.

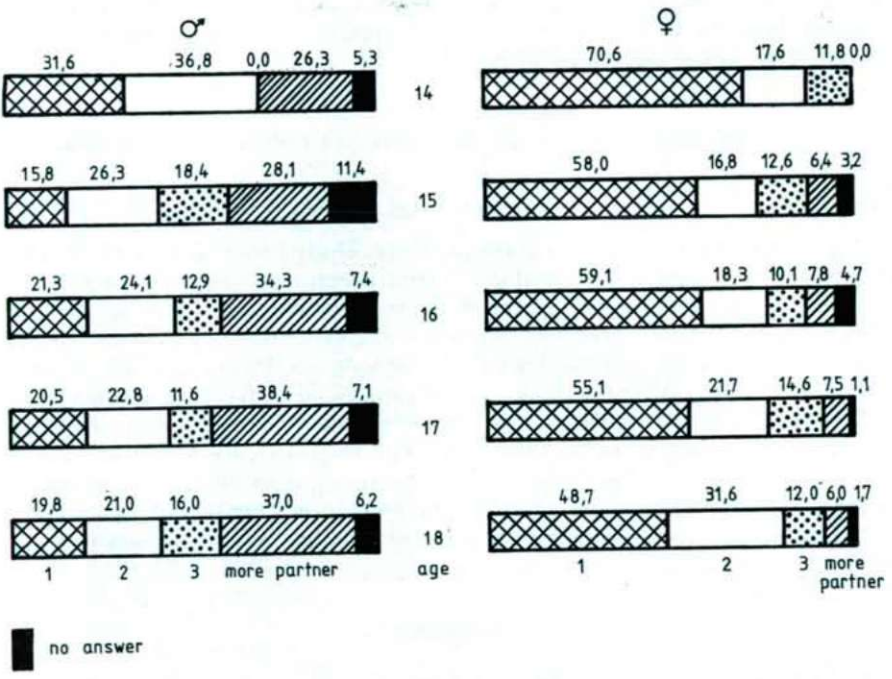

Fig. 2. Frequency of the number of the number of partners o(students having sevetal sexual intercourses (in %) .(boys: n=651; girls: n=787)

CAUSE OF ACCELERATED SEXUAL LIFE OF THE YOUTHS

Our data unambigously indicate the acceleration of the sexual life of the young people, the causes of which could be the followings according to our opinion, apart from the more rapid biological maturity:

1. Sexual education does not keep pace with the accelerated biological rhythm. The majority of parents do not take into consideration that the sexual demand of their children has reasonable base. Thus the young are compelled to develop sexual behaviour forms themselves, sometimes on the basis of "patterns" and "fashions" prevailing in peculiar transfers (PIAGET, 1970).

2. Though biological maturity shifted to an earlier period, social development takes place later and thus the lengthened time interval parctically enhances the sexual inclination. This is promoted by the ambition of the young to become independent as well as by the conflict-state of their emotive detachment from parents.

3. As the result of the "scientific fight" against the socially established inhibitions the satisfying self-fulfilling and communicative character of the sex act gains more and more ground.

4. Sexual relations are ensured relatively soon in the life of the young people during the course of acquaintance. The short period does not give possibility for the appropriate levelled development of emotions, thus the individual satisfaction prevails in the sexual relations. By this means, the sex act appears as biological demand only and does not serve as the deepening of emotions.

5. The more enhanced eroticism of everyday life.

6. The better assurance of contraception increasingly reduces the inhibitions existing in this field.

7. The strong decrease of virginity, as status symbol.

The acceleration of the young people's sexual life raises serious biological and social problems. Despite the general use of contraceptives (their use during the course of mating was 45.1% in the case of the students occurring in our sample) the number of unwanted preganacies, procured abortions and other health problems has increased. The psychical consequences implied in the long run by exaggerated are also not minor, many times impersonal sexual relations, devoid of required emotional bases.

It belongs to the complexity of the problem, however, that after all, the relations with the other sex are socially determined. The responsibility lies on the adults — writes LÖWE (1965) —, in the world of whom the young grow up and live, whose books they read, films they watch and whose sexual morals they see before themselves. The sexual education of the young people also necessitates the sexual education of the adults.

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SHORT COMMUNICATIONS

THE IMPORTANCE OF THE SPORE-POLLEN INVESTIGATIONS IN THE RECOGNITION OF THE RADIOACTIVE ELEMENT CONTENT OF THE LAKE MUD

M. KEDVES and T. SZEDERKÉNYI

(Received: May 11, 1984)

During the investigations of plant remains of the sediments of lake Vadkert (Soltvadkert), we recognized the opportunity of the occurrence of radioactive elements in the mud of the lakes of the Hungarian Great Plain. The basic idea came by the presence of dark brown colored vegetal tissue remains together with colourless holocene sporomorphs, fungal, algal and other plant remains. This phenomenon may have several reasons, but this may be in consequence of the rebedding of radioactive material too. The Radiometric Laboratory of the Experimental and Research Factory of the Ore Mining Company of Mecsek analyzed six mud samples and demonstrated in each a measurable quantity of radioactive materials (U: 0.9—$1.3.10^{-4}$%, U-Ra equ.: 0.9—$1.5.10^{-4}$%, Ra: 3.1—$5.1.10^{-13}$%, Th: 6—13.10^{-4}%, K: 0.6—0.7%). We express our thanks for the Laboratory for this important contribution.

The importance of the plant microfossils in the sandstone-type uranium deposits was reviewed by NORRIS and EDMOND (1973). On the basis of this work we emphasize the following: Uranium and geochemically allied elements are transported in ionic or complexed form an alkaline slightly reducing aqueous medium. P. 128: "Precipitation of these elements as complex mixtures of oxides and sulphides takes place at sites of strongly reducing conditions which may be either fixed or transient." P. 129: "The main mechanism of ore mineral precipitation is H_2S generated in prodeltaic sediments or by petroliferous accumulations." ... "particularly noticeable in regard to U/V or U/Cu rations. In general the main extrinsic heavy elements are uranium with one or more of V, Fe, Mn, Cu, Mo, S, As, Se, Co, Ni (HEINRICH, 1958; SHOEMAKER et al., 1959). Thorium is absent as it does not form a soluble ion analogous to the uranyl ion." P. 130: "Mineralogy and mineral paragenesis are complicated and variable (HEINRICH, 1958; LAVERTY and GRASS, 1956; WEEKS, COLEMAN and THOMPSON, 1959)...". P. 131: "In a series of experiments SZALAY (1954, 1957) demonstrated that uranium fixation in carbonaceous sediments is related to adsorbtion of uranium from solution by cation exchange of uranyl ions with hydrogen ions in humic acid." P. 132: ..."woody tissue is an important source of humic acids capable of fixing uranium, as the well-known relationship between macroscopic fossil wood and uranium attests."

This question has two major fields: a geochemical, and a biological one. We project to work on the problems in both fields. Methodical problems are especially emphasized. As regards the biological effect of the radioactive mud as most important

problems the following may be pointed out: 1. The effect of the phyto- and zooplancton. 2. Cytological investigations on the roods, and other vegetative organs of the angiosperm taxa. 3. The palynological study of the recent taxa may render information about polyploidity. 4. The TEM study of the pollen grains of the radioactive material containing mud may prove whether in natural environment sporopollenin adsorps uranyl ion what may change the electron scattering power of the exine. 5. The biological testing of the radioactive material seems to be an interesting field of investigation. 6. Finally, we call attention for the study of the curative effect of the radioactive mud of the lakes of the Great Hungarian Plain.

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GREGUSSISPORITES, A NEW SPORE GENUS FROM ALBIAN SEDIMENTS

M. JUHÁSZ and S. B. SMIRNOVA

(Received: September 30, 1984)

Genus: **Gregussisporites** gen. nov.

Derivatio nominis: The name has been given to honour PROF. DR. PÁL GREGUSS

Type species: *Gregussisporites orientalis* nov. gen. et nov. sp.

Diagnosis: trilete spores with subcircular to subtriangular amb. Both proximal and distal surfaces ornamented by large verrucae which are regularly hexagonal in outline at their bases, forming a honeycomb-like " negative reticulum."
Differential diagnosis: The new genus is distinct from *Tuberosisporites* DÖRING 1964, *Varirugosisporites* DÖRING 1965 in having regularly distributed verrucae and honeycomb-like "reticulum".

Gregussisporites orientalis nov. gen. et nov. sp.
Plate I., Figs. 1—5.

Locus typicus: Súr, Mts. Bakony (Hungary), Bore Súr-1.
Stratum typicum: "Munieria" clayey-marl, Tés Clay Formation, 533 m. Middle Albian.

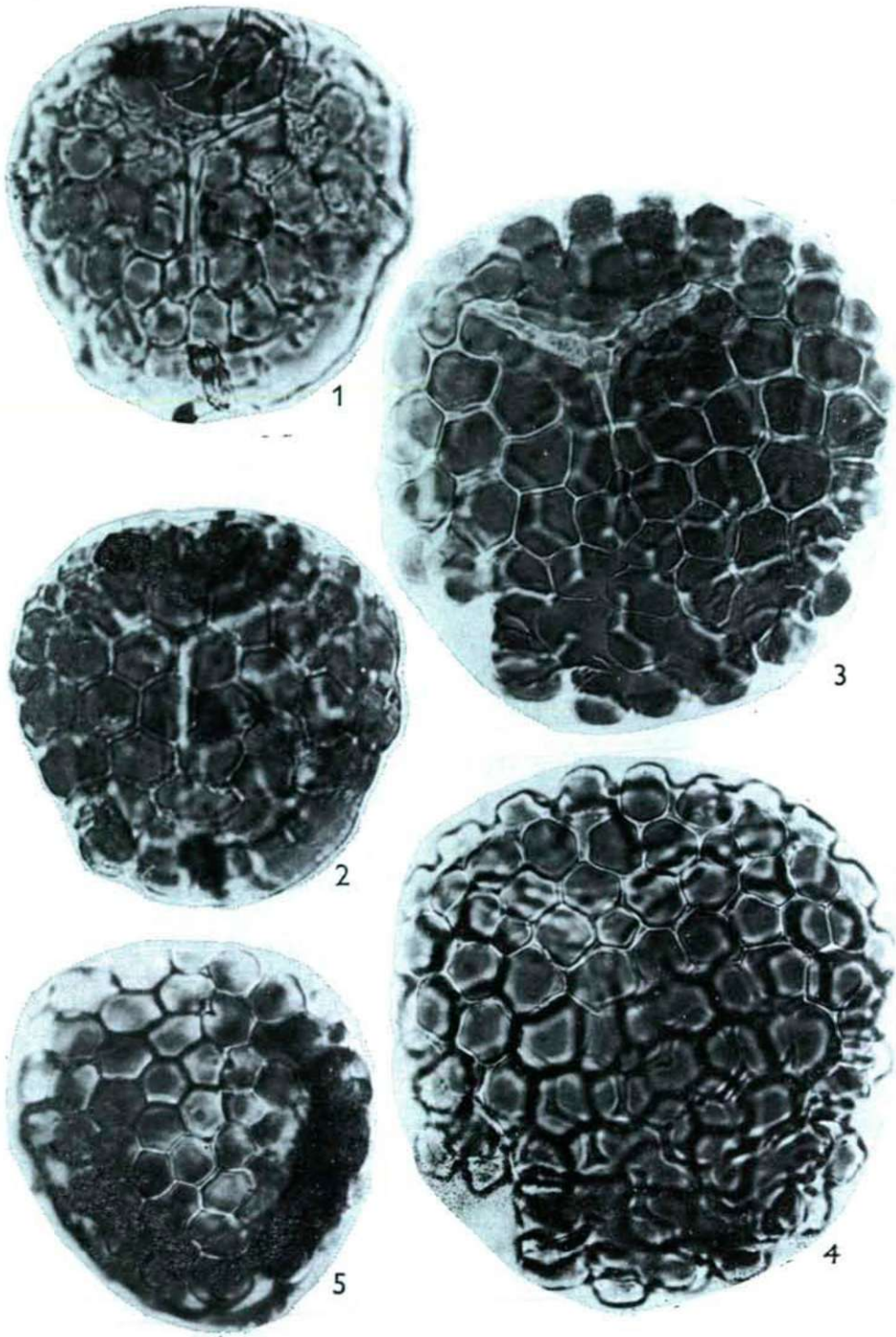
Holotype: Slide: Súr-1.: 533/1., coord.: 37.1—113.2. Pl. I., Figs. 1—2.
Paratypes: Mts. Crimea (USSR), slide M-1.; coord.: 45.7—104. Pl. I., Figs. 3, 4., and slide 5G., coord. 40.5—107., Pl. I., Fig. 5.

Diagnosis: Trilete spores, laesurae simple, short, about 1/2 of spore radius, are often opened. Amb subcircular or rounded subtriangular. Exine 5—7 μm thick, verrucose on distal as well as proximal face. Verrucae hemisphaerical, 7—10 μm in diameter at their bases, 4—6 μm high, spaced 0.7—1.0 μm apart, formed more or less regularly hexagonal, honeycomb-like negative reticulum.
Spore size: 48—80 μm (holotype: 52 μm).

Differential diagnosis: the *Gregussisporites orientalis* nov. sp. differs from all verrucose species in having honeycomb-like negative reticulum both on proximal and distal surfaces.

Occurrence: Hungary: Mts Bakony, Middle Albian to Upper Albian; rare species.
USSR: Mts Crimea, Upper Albian; common.

Plate I



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CHRONICLE
1984

Personalia

A memorial tablet was inaugurated on September 21, 1984 on the occasion of the 5th anniversary of the death of Dr. Imre Horváth, late professor and department head, by the Attila József University on the wall of the Phytotron building located in the Botanical Garden. Dr. Imre Horváth was director of the Botanical Garden and the Department of Botany of the Attila József University between 1965—1979. The inauguration address was held by Dr. Sándor Gulyás, senior lecturer.

Organization of the Assotiation of the Societies of Technology and Natural Sciences of the County of Csongrád, Section of the Hungarian Society of Biologists of the County of Csongrád, the Szeged-County Municipal Council and the Attila József University inaugurated a memorial tablet on September 22, 1984 on the event of the centenary of the birth of Dr. Béla Farkas, late professor and department head of the Department of Zoology of the Szeged University of Sciences. The memorial tablet was placed on the wall of his former house (Szeged, Hunyadi János avenue 43). The commemoriation was inaugurated by Dr. Jenő Bátyai, vice-president the Association of the Societies of Technology and Natural Sciences of the County Organization of Csongrád. The inauguration address was held by Professor Dr. Ottó Fehér, the tablet was taken over (on behalf of the city) by Mrs. Dr. József Müller, vice-president of the Council.

Scientific degrees

The degree of candidate in biological sciences was obtained by:

Dr. Antónia Marcsik (Department of Anthropology) with her dissertation: "Paleopathology of the Avar-age between the Danube and the Tisza",

Dr. J. Nemcsók (Department of Biochemistry) with his dissertation: "Effect of environmental contamination on certain biochemical and physiological processes in carp, silver carp and silure", and

Dr. Mária Nagy (Department of Plant Physiology) with her dissertation: "Hormonal regulation of the dormancy and germination of seeds demanding stratification".

Nominations

DR. F. ZSOLDOS was appointed to professor of the Department of Plant Physiology by the Cabinet Council.

The Minister of Cultural Affairs appointed DR. L. ERDÉLYI and DR. P. MARÓTI to senior lecturers, former at the Department of Comparative Physiology, latter at the Department of Biophysics.

Professorship

The Minister of Cultural Affairs conferred the title of university professor on DR. M. KEDVES, scientific advisor (Department of Botany).

Awards

PROFESSOR DR. L. FERENCZY received an academic award.

Varia

On the 10th December, 1984 as guest of the Attila József University PROF. DR. H. WALTER, (the head of the Department of Humanbiology and Anthropology, Bremen, West Germany) gave a lecture entitled "Races, castes, peoples and cultures in India. Results of anthropological investigations" and PROF. DR. V. P. CHOPRA (Department of Anthropology, Hamburg, West Germany) also pronounced a lecture entitled "Population structure and microevolution with reference to Indiae"

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Készült monó szedéssel, íves magasnyomással, 19,6 (A/5) ív terjedelemben,
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